



Royal Netherlands Institute for Sea Research

A multidisciplinary approach to pattern formation in ecology

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From simple to simpler

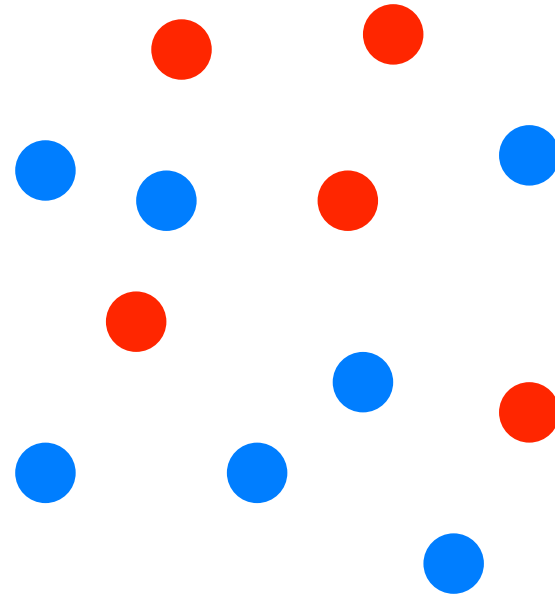
Spatial Ecology

Ecological simplification



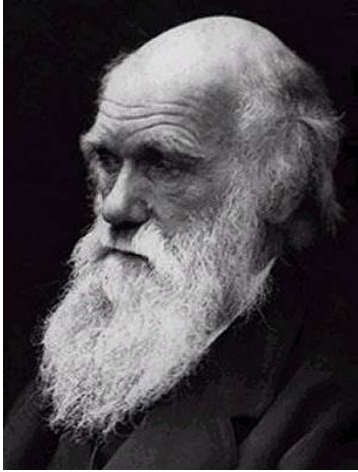
A plant-herbivore system

Physical simplification



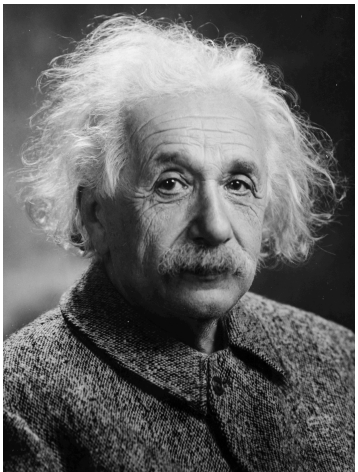
A plant-herbivore system

Our own heros



Darwin

- Natural selection acts on the total of all traits that shape an individual.
(Holistic perspective)



Einstein

- Explain everything from first principles, using the simplest possible explanation.
(Reductionistic perspective)

Marrying physics and ecology a study of pattern formation by mussels

Spatial Ecology





A case study on mussel beds

Spatial Ecology

Mussel beds in the Wadden Sea



Scale: \pm 200 m wide



Mussels close by

Competition



Facilitation



Scale-dependent feedback



Pattern formation in mussels





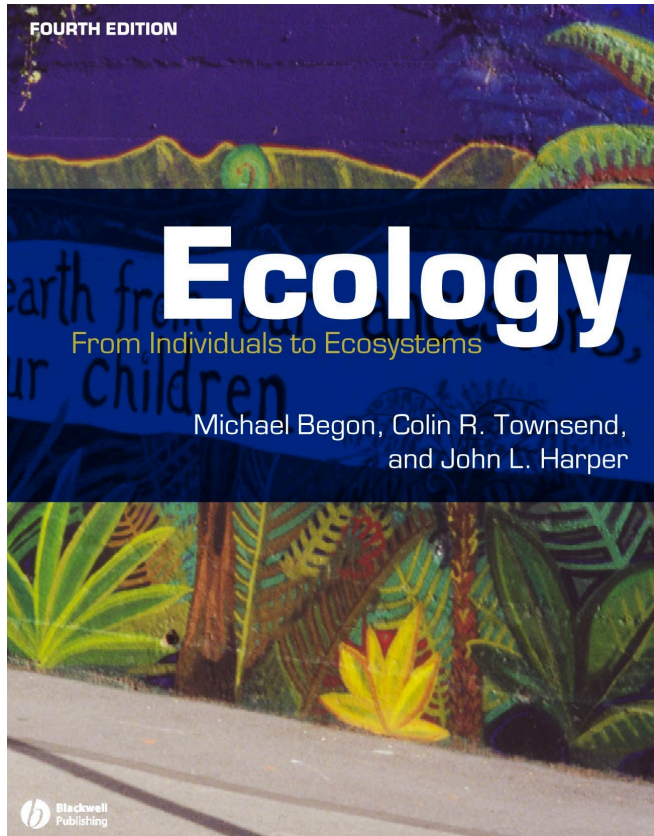
- Understanding the movement of individual mussels



- Understanding mussel pattern formation –> Self-organization



- Emergent properties of complex systems – for real!



Typical ecological model:

$$\frac{\partial n}{\partial t} = f(n, \dots) + D \frac{\partial^2 n}{\partial x^2}$$

**Growth /
mortality**

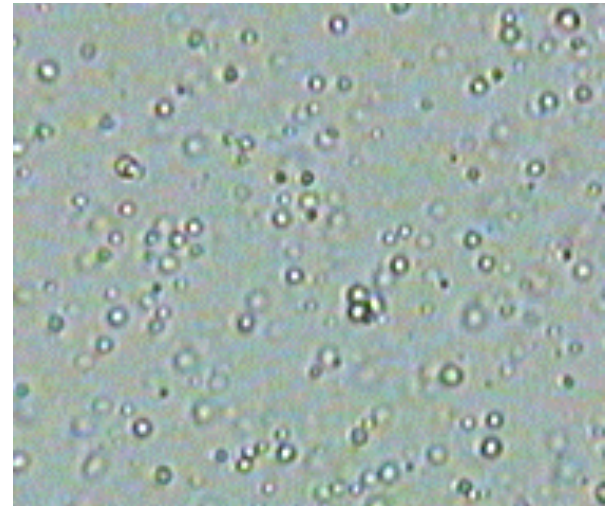
**Dispersion
term**

Brownian motion



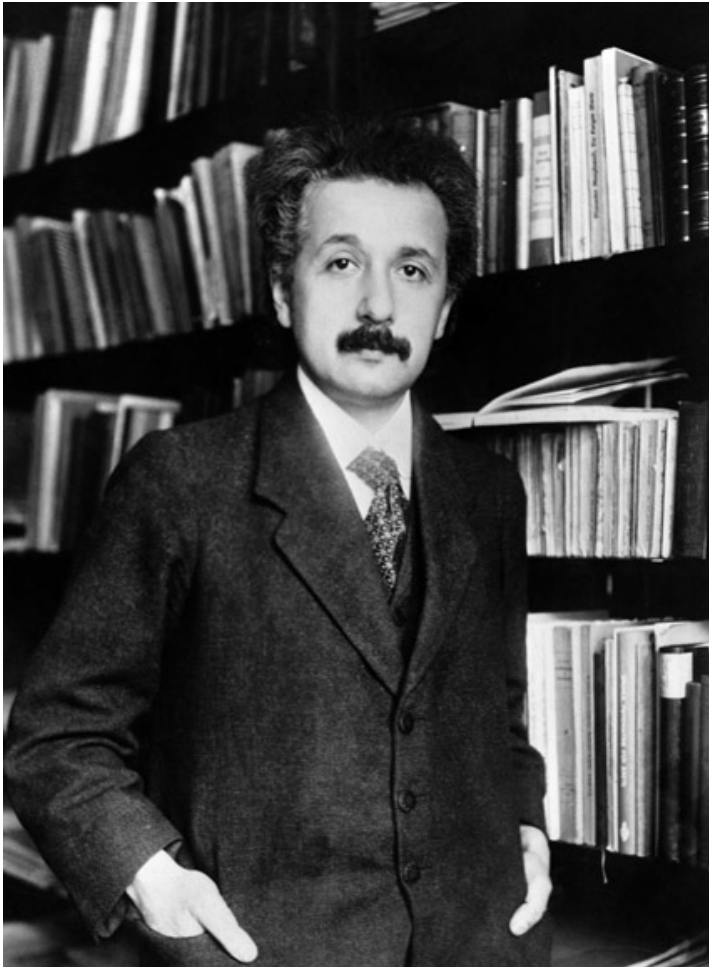
Robert Brown (1773 – 1858)

- Erratic movement of particles in a solution when watch through the microscope.



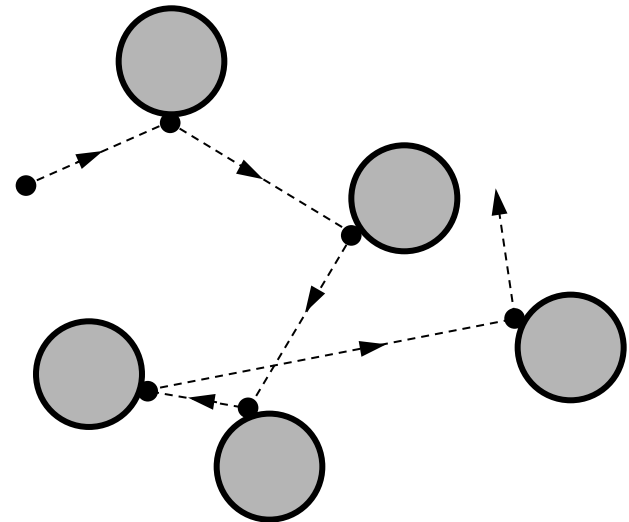
Einstein's theory

Spatial Ecology



Einstein, 26 years old in 1905

- Particles are bombarded by water molecules.



$$\text{Diffusion} \approx D \frac{\partial^2 n}{\partial x^2}$$

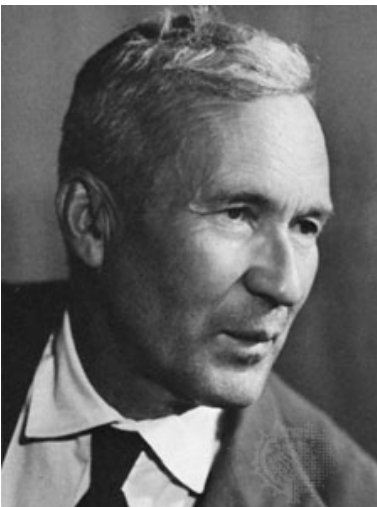
Einstein, A. 1905 Annalen der Physik. 322, pp 549–560.

Picked up by biologists

Spatial Ecology



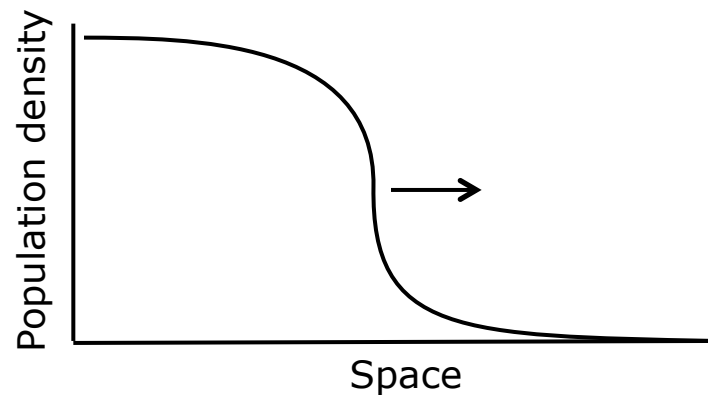
Ronald Fisher



Andrey Kolmogorov

- Fisher-Kolmogorov equation (1937)

$$\frac{\partial n}{\partial t} = n(1-n) + D \frac{\partial^2 n}{\partial x^2}$$



- The first use of diffusion equations in ecology, to attempt to calculate the rate of invasion of specific genes within populations.

Simple or complex

Spatial Ecology

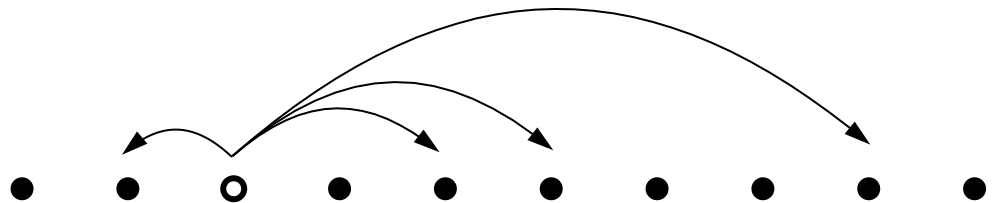


Paul Pierre Lévy
(1886 – 1971)

- Brownian walk:
only short-range movement



- Lévy walk:
also long-range movement

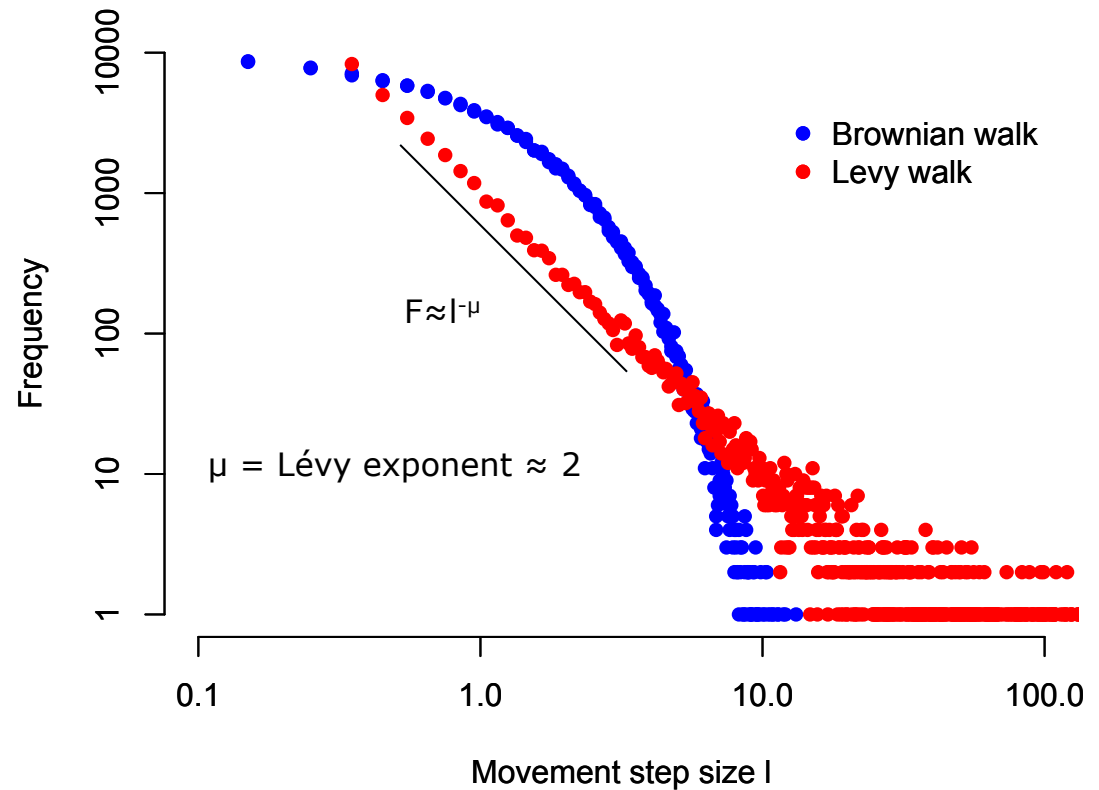


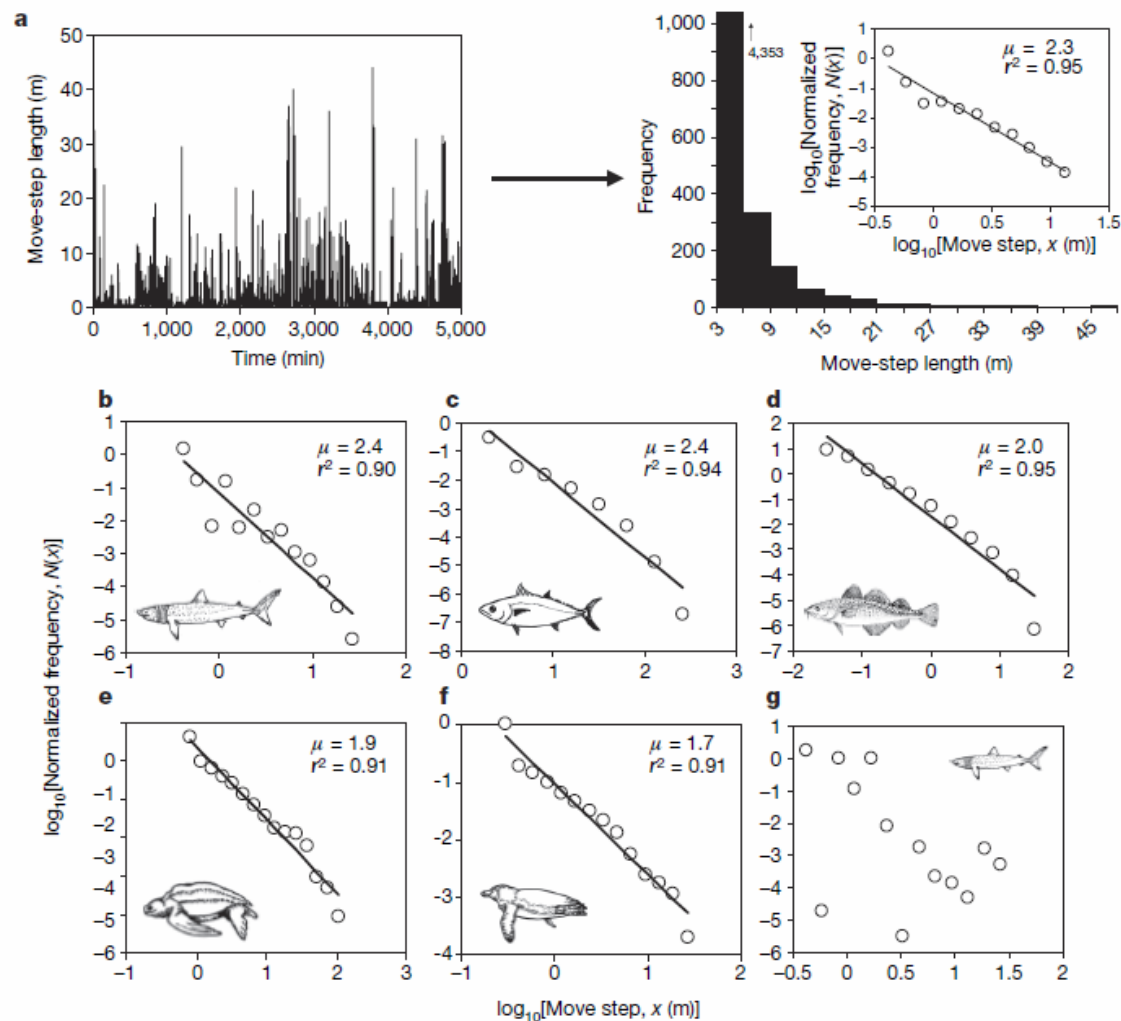
Lévy flights – how to see?

Spatial Ecology



Paul Pierre Lévy
(1886 – 1971)





Sims *et al.* (2008):

Lévy walk found in a range of marine predators.

What “move” do mussels do?

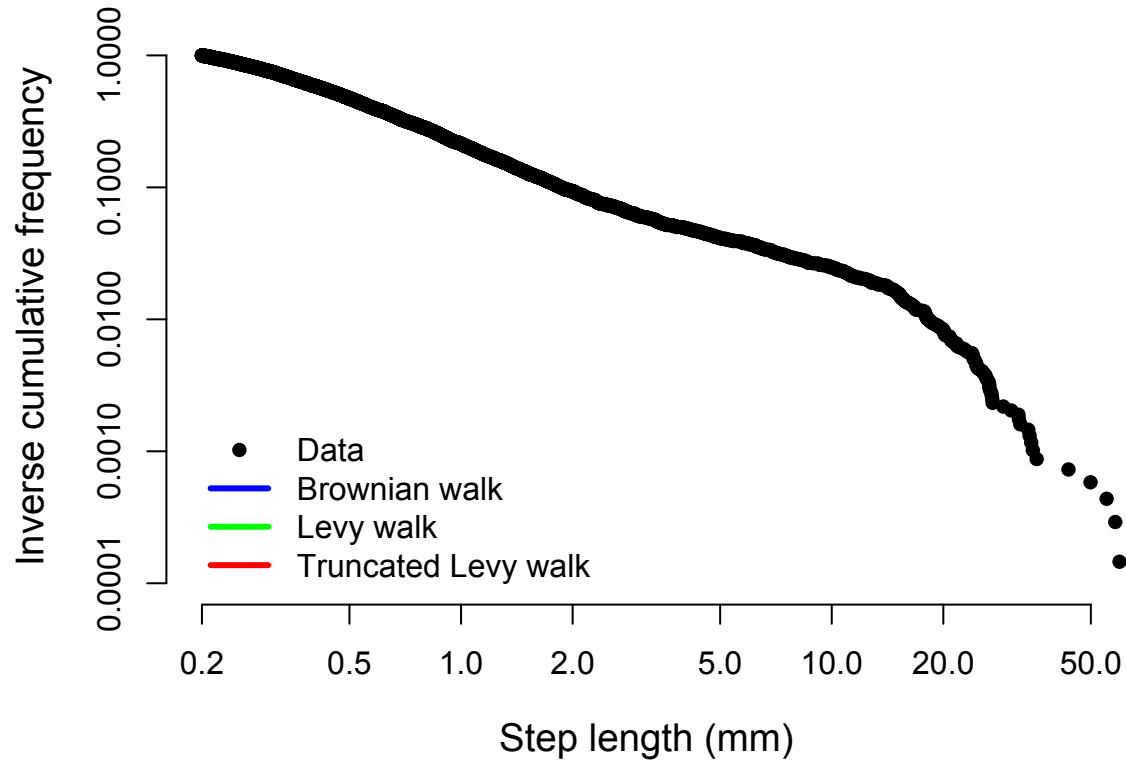


PhD work of
Monique De Jager

Movie:
Aniek van der Berg

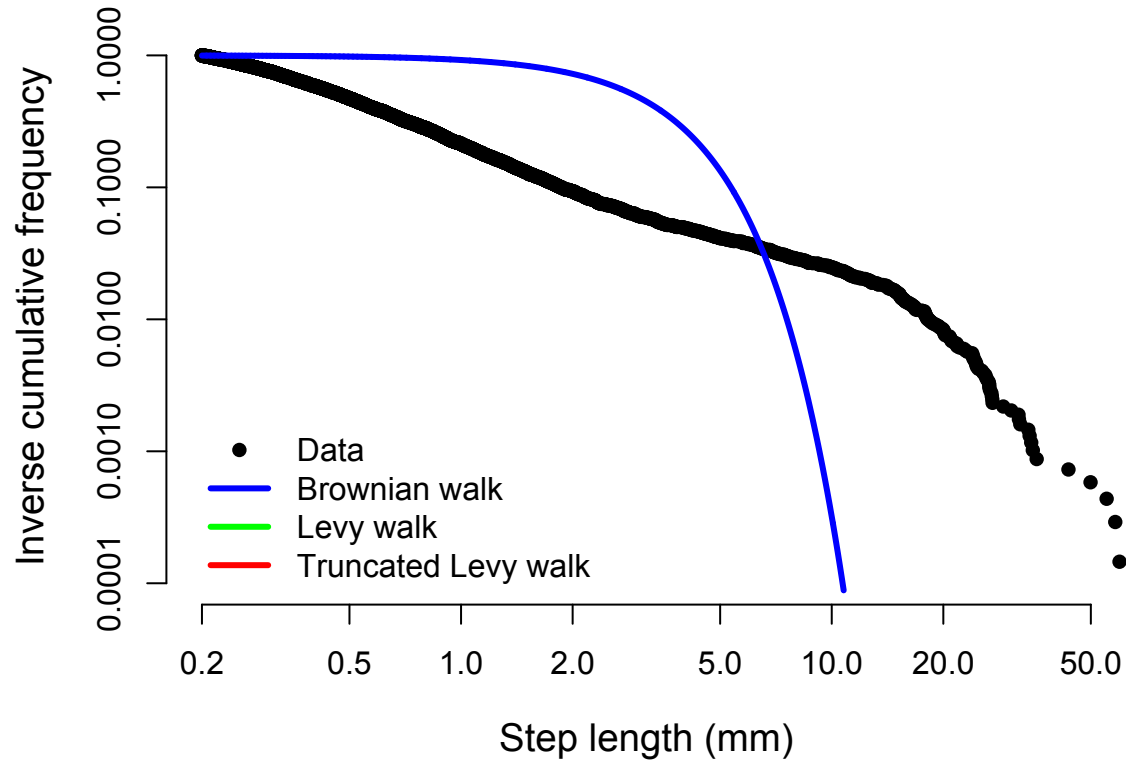
What “move” do mussels do?

Spatial Ecology



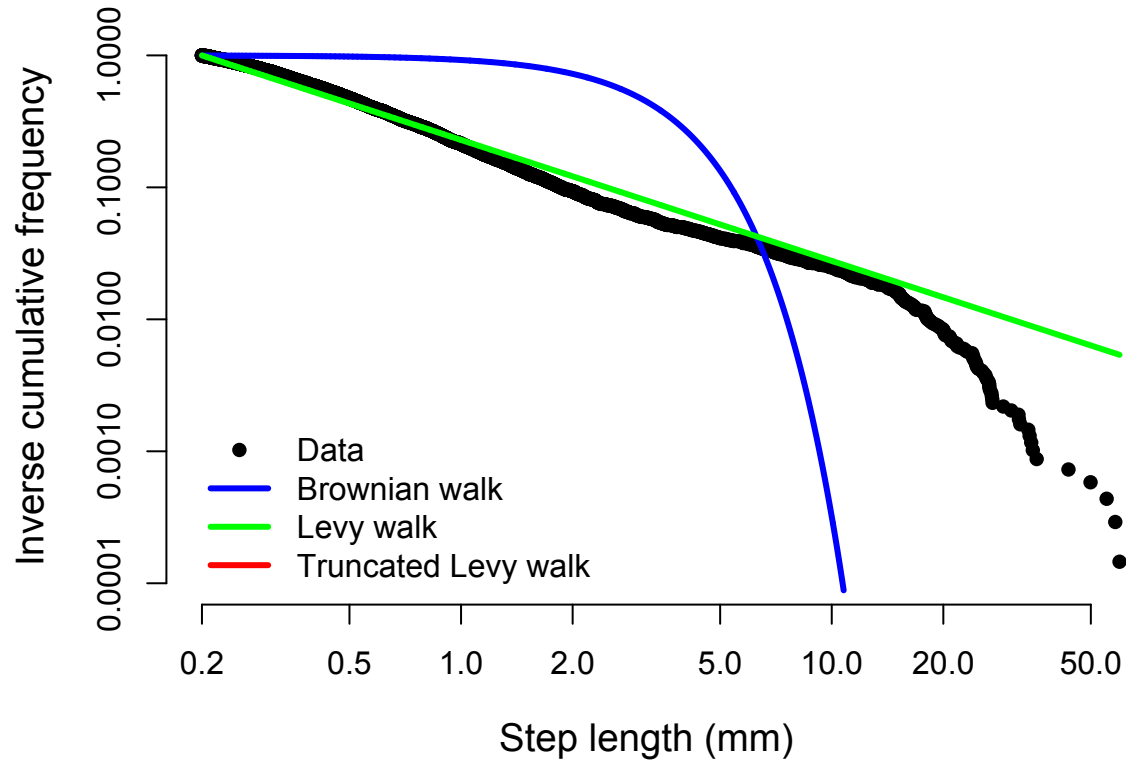
What “move” do mussels do?

Spatial Ecology



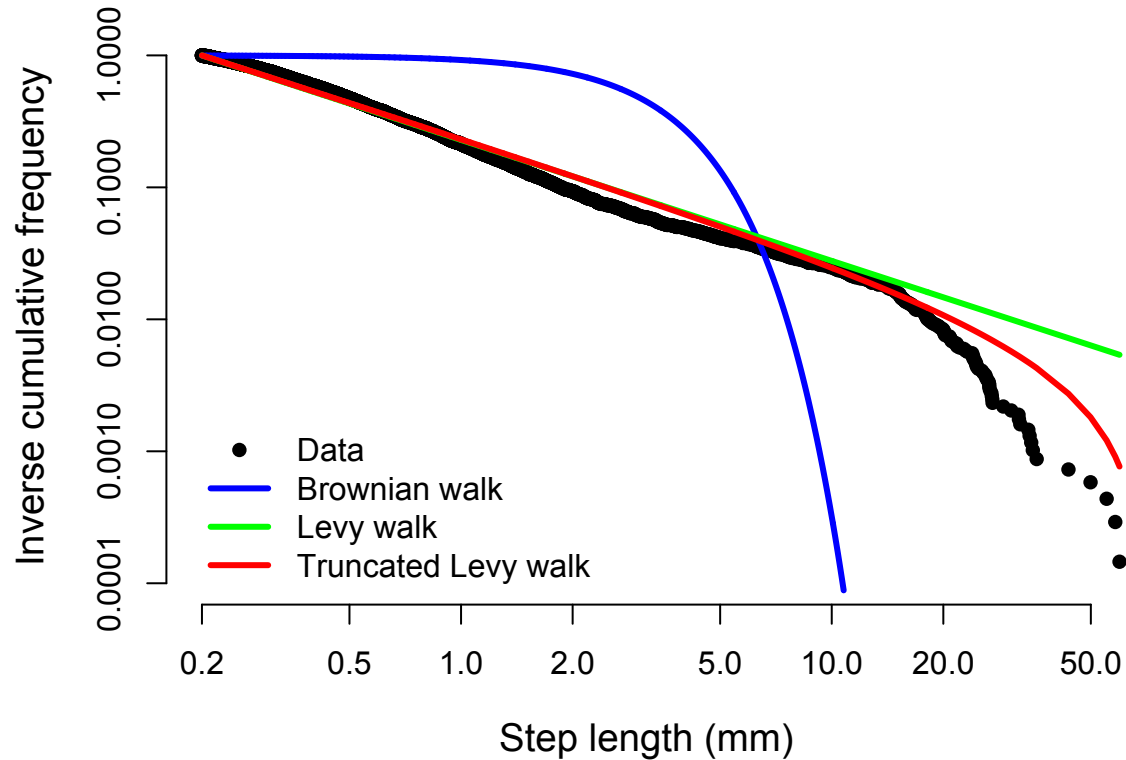
What “move” do mussels do?

Spatial Ecology



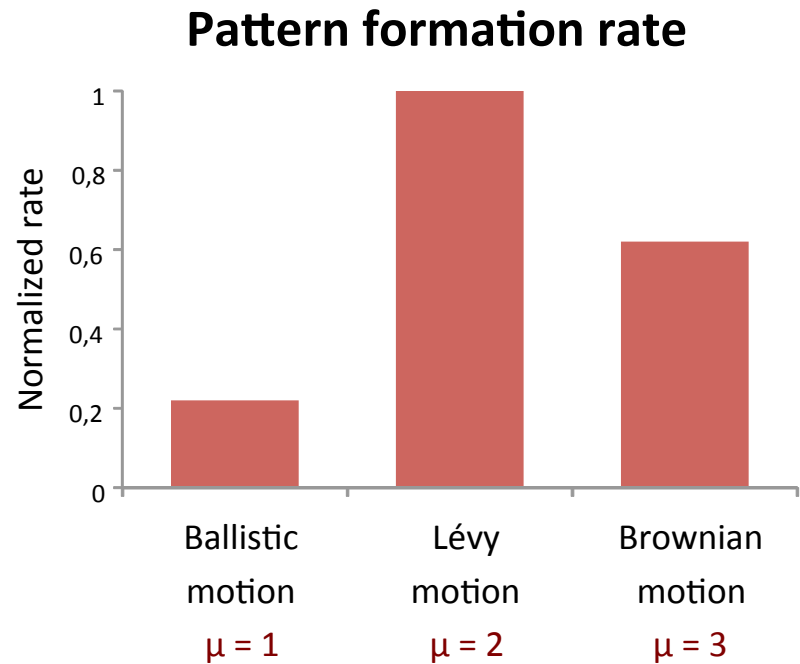
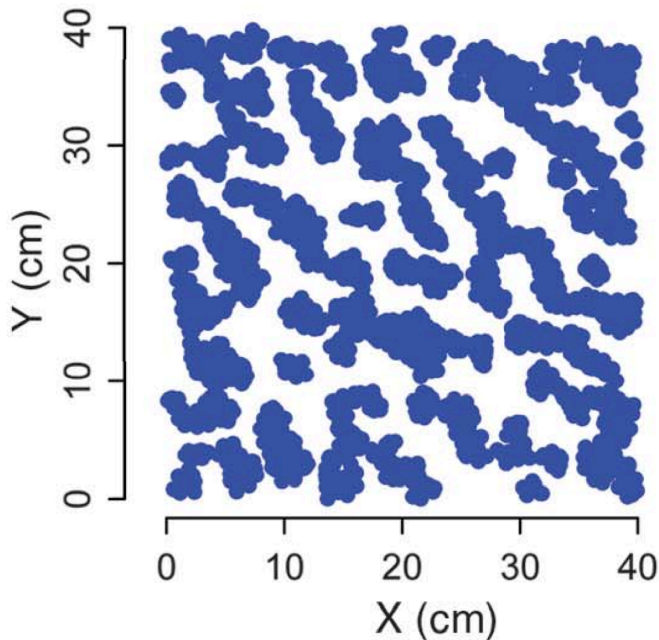
What “move” do mussels do?

Spatial Ecology

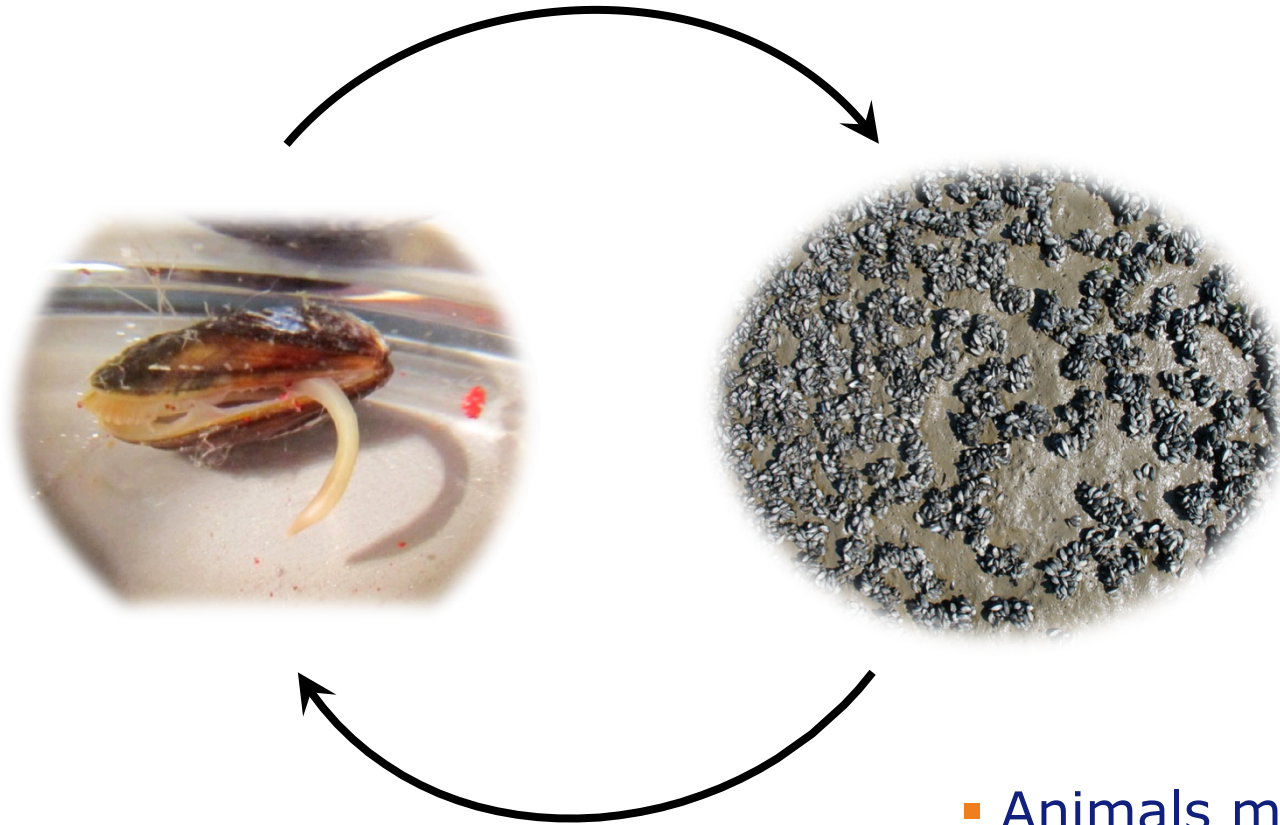


Mussels are doing a Lévy walk!

Model results: Lévy walk most efficient for pattern formation



Feedback between animal movement and complexity



PhD work of
Monique De Jager

- Animals may themselves create the conditions for Lévy walks to be adaptive.

Humphries, Sims *et al.* (2010):

- Lévy walks found in marine predator movements when prey density is low.
- But: Brownian walks when prey density is high!





De Knecht *et al.* (2007, Behavioral Ecology):

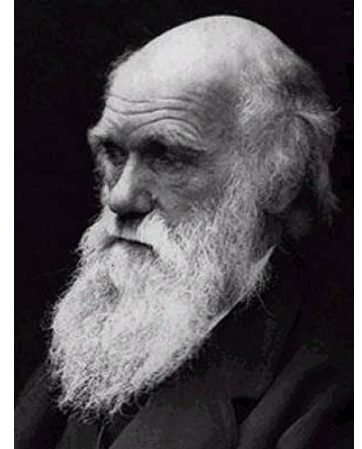
- Lévy walks found in goat movements when browse density is low.
- But: Brownian walks when browse density is high!

- Other studies with similar conclusions: Bartumeus *et al* 2003

How to explain Brownian motion

- **Adaptation:**

- Do organisms adapt their movement strategy to new conditions?

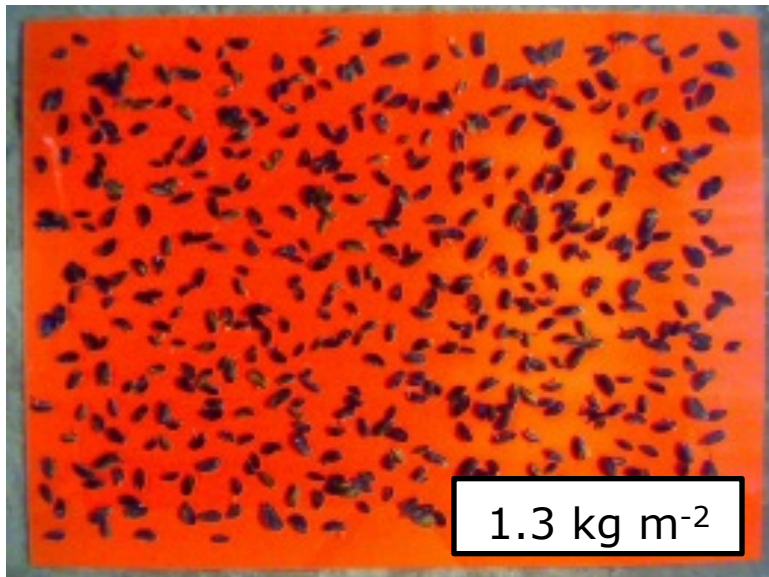


- **An ecological process:**

- Does it results from interaction with other organisms?



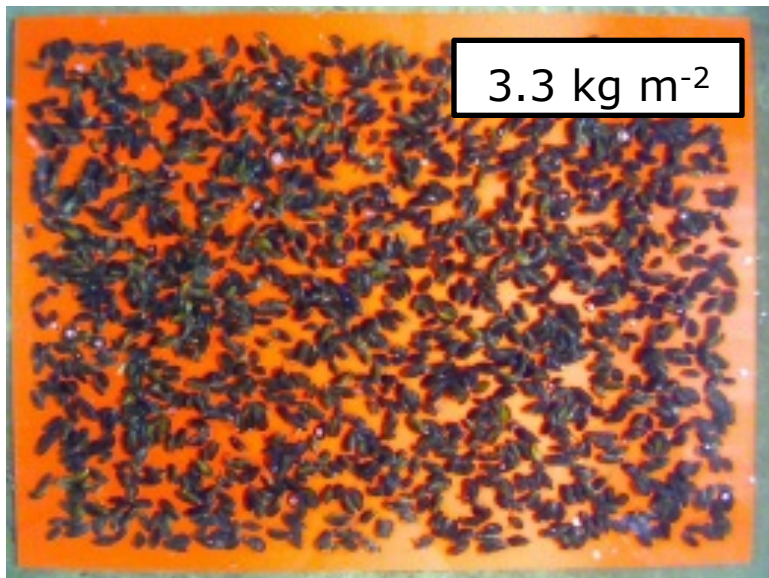
How to analyse this in tracked animals?



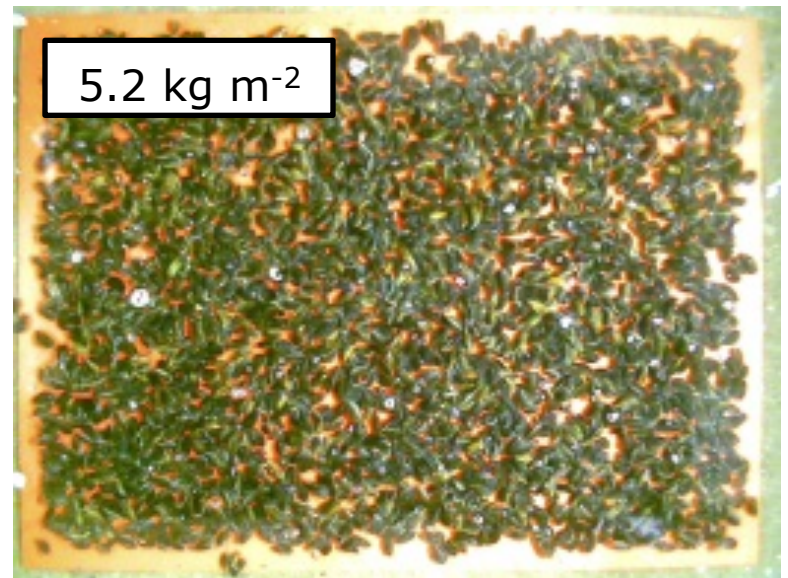
1.3 kg m⁻²



2.0 kg m⁻²



3.3 kg m⁻²



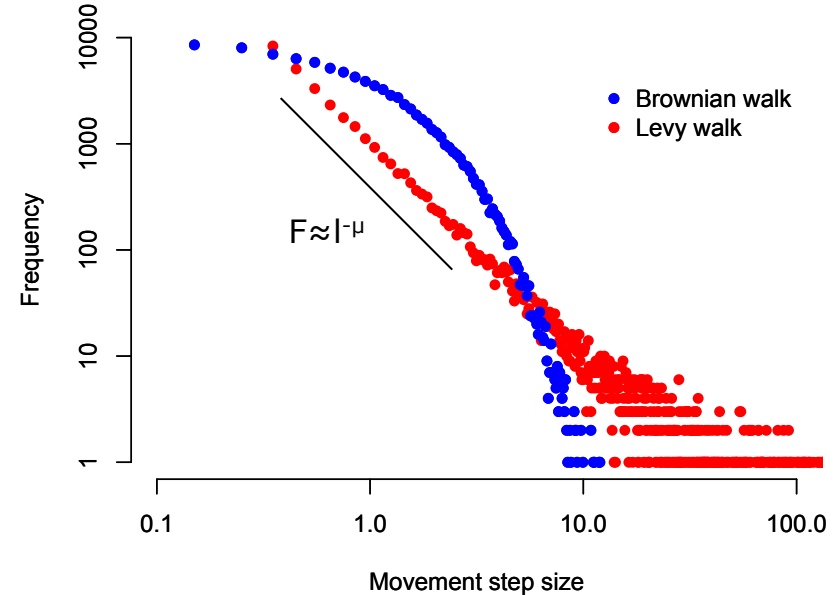
5.2 kg m⁻²

Lévy flights – how to see?

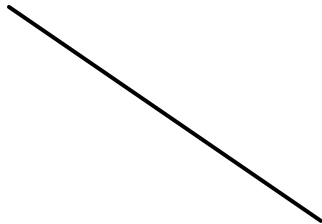
Spatial Ecology

Power function: $F(l) = C \cdot l^{-\mu}$

- $\mu \rightarrow 1$: Ballistic motion
- $1 < \mu < 3$: Lévy walk
- $\mu \geq 3$: Brownian walk

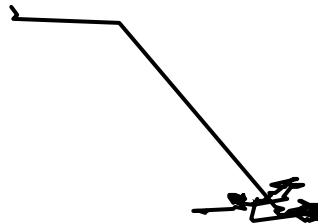


Ballistic walk



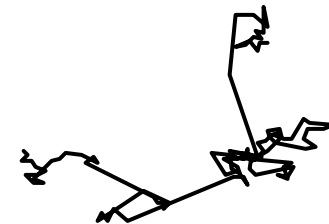
$$\mu = 1$$

Lévy walk



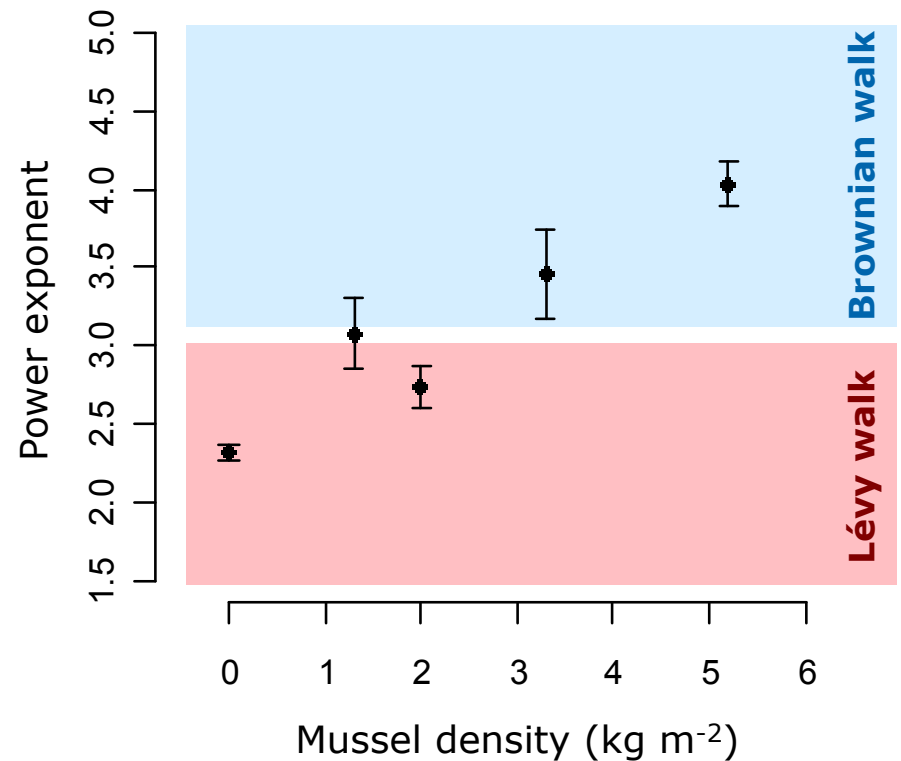
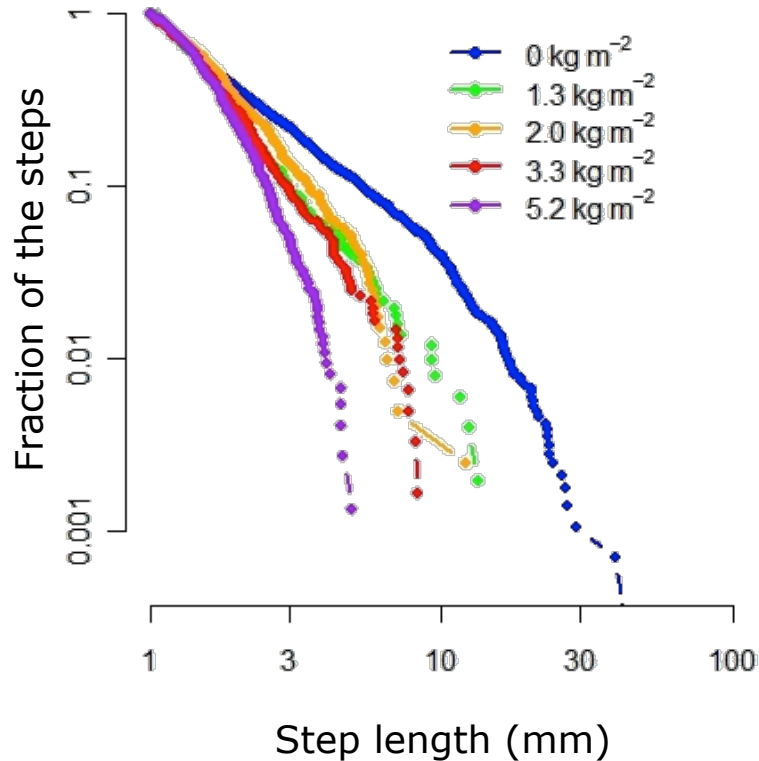
$$\mu = 2$$

Brownian walk



$$\mu = 3$$

Observed movement pattern changes with mussel density



Clash of the titans...

Spatial Ecology

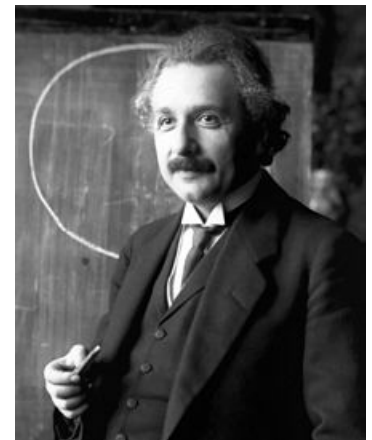
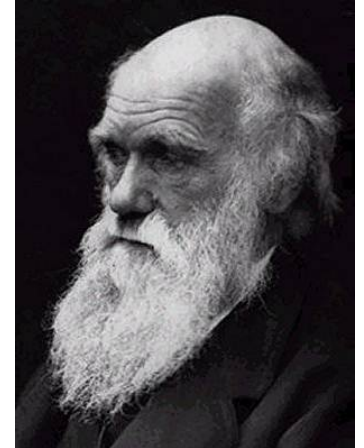
Is it adaptation or physics?

Adaptation (biology):

- Mussels change their overall movement to a Brownian walk

Physics:

- Mussels want to do a Lévy walk, but bump into other mussels.
- ➔ Unhindered mussels still do a Lévy walk

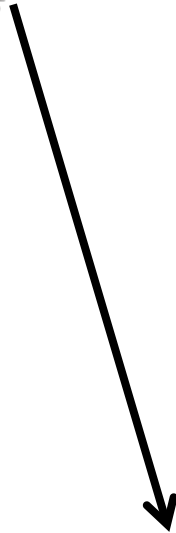
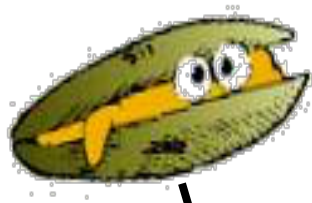




Spatial Ecology

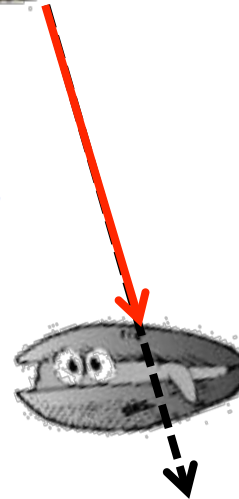
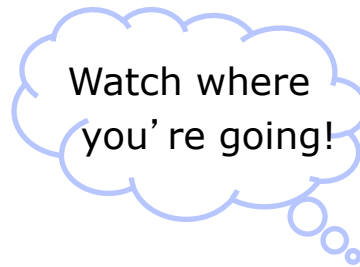
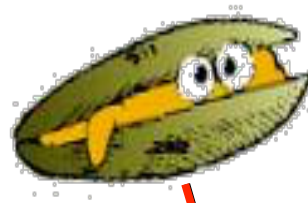
Separate truncated from non-truncated steps

**Non-truncated
steps**



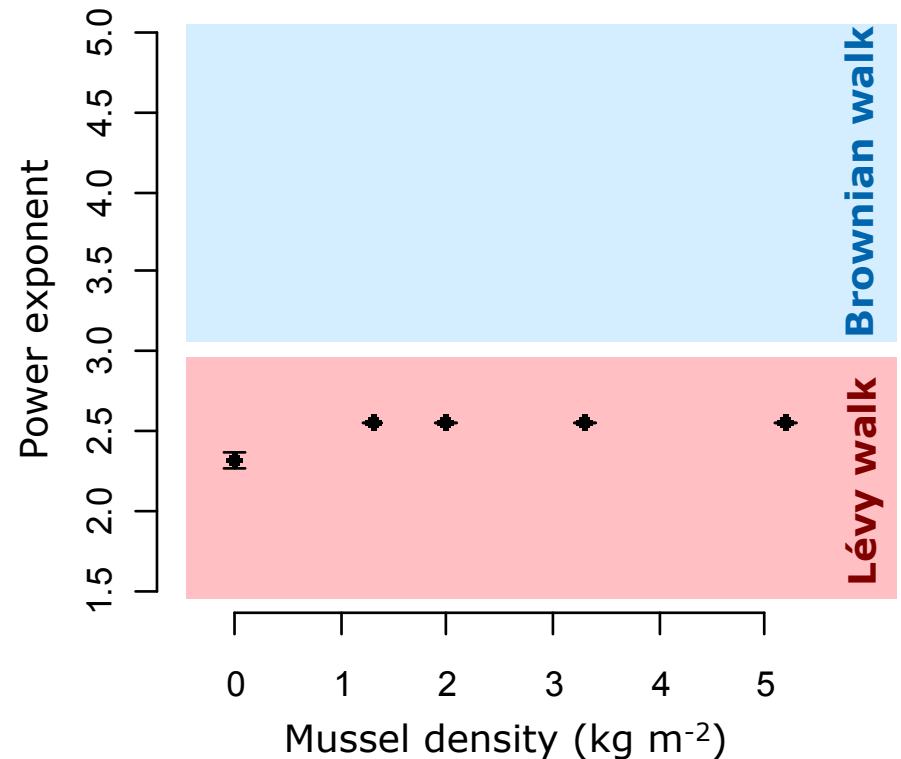
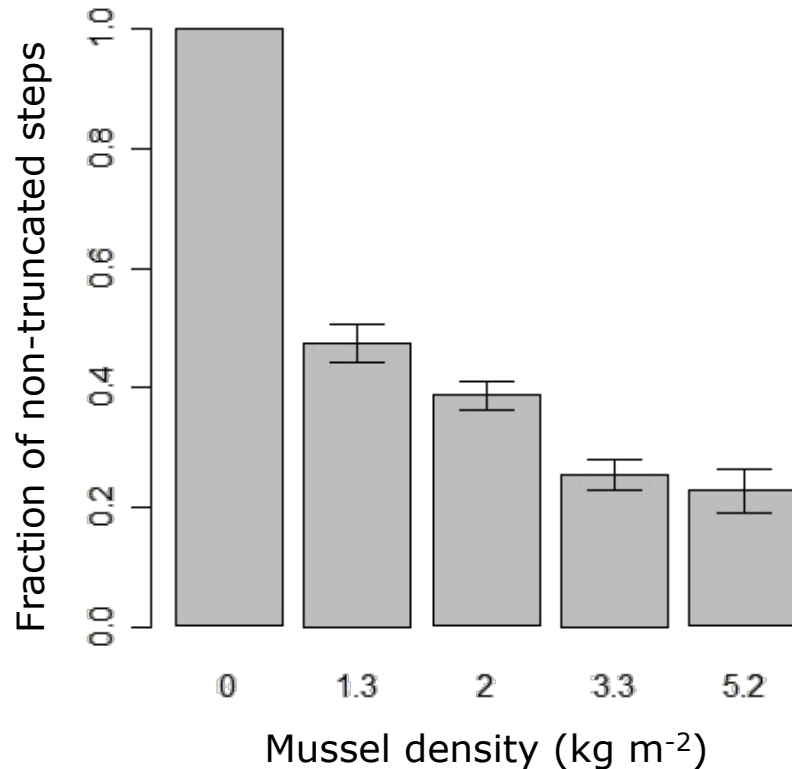
Free space

**Truncated
steps**



PhD work of
Monique De Jager

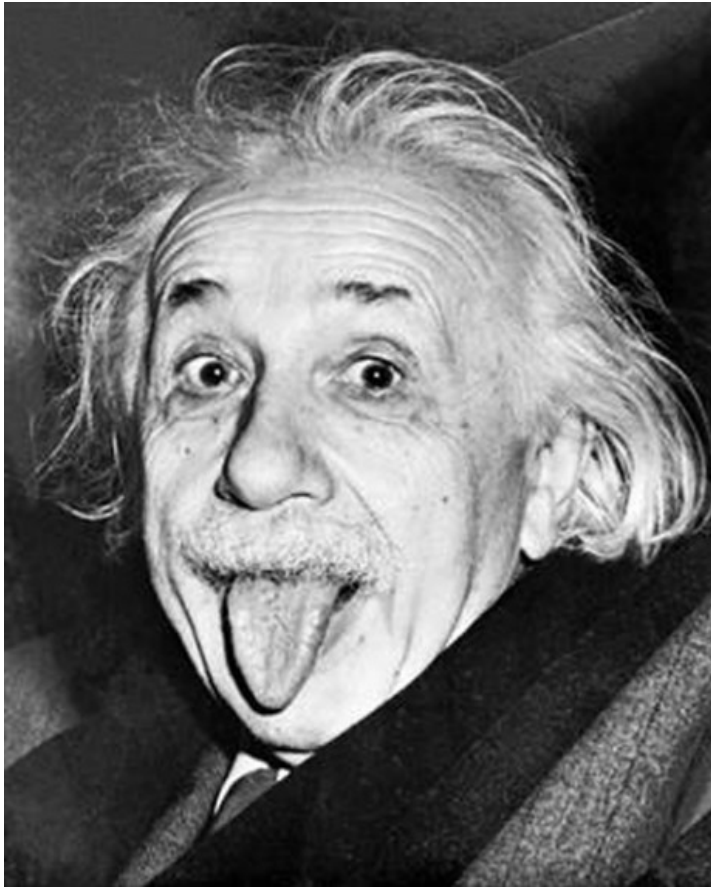
Non-truncated steps only: no change in movement pattern



Implication:

Truncation of steps results in Brownian motion!

Physics kicks in at high density

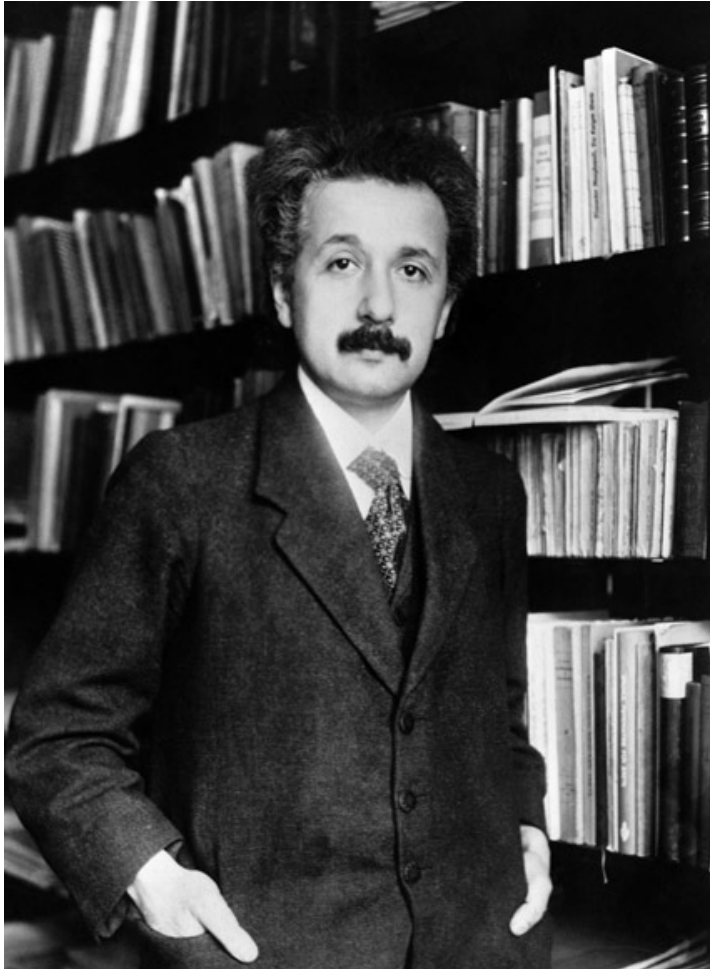


- Encounters between mussels, rather than adaptation, explains Brownian motion in mussels.

→ **Einstein's explanation!**

Einstein for ecologists

Spatial Ecology

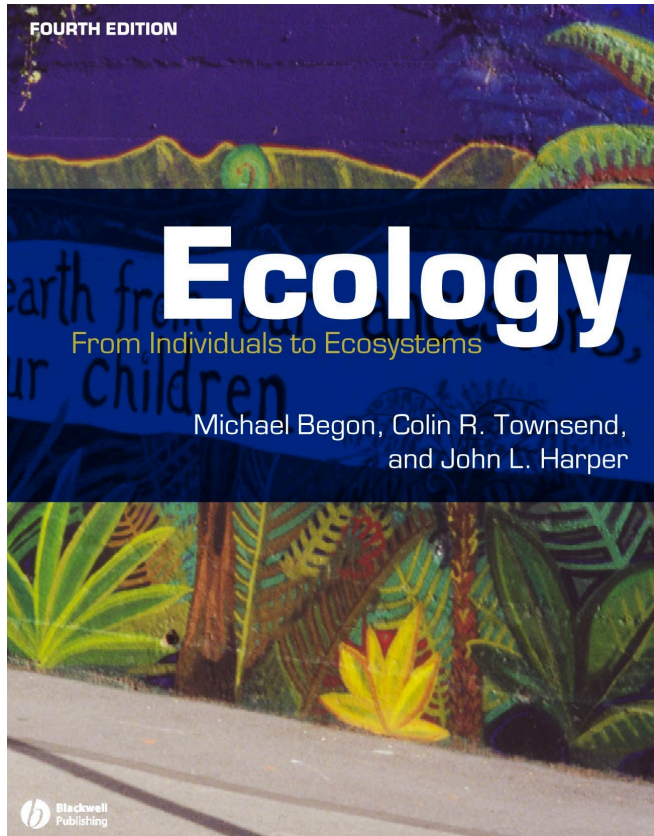


Interactions (encounters) between organisms shape their **movement**.

- Food encounter
- Predator encounter
- Interference
- Physical hindrance

High encounter rate

→ Brownian motion



Typical ecological model:

$$\frac{\partial n}{\partial t} = f(n, \dots) + D \frac{\partial^2 n}{\partial x^2}$$

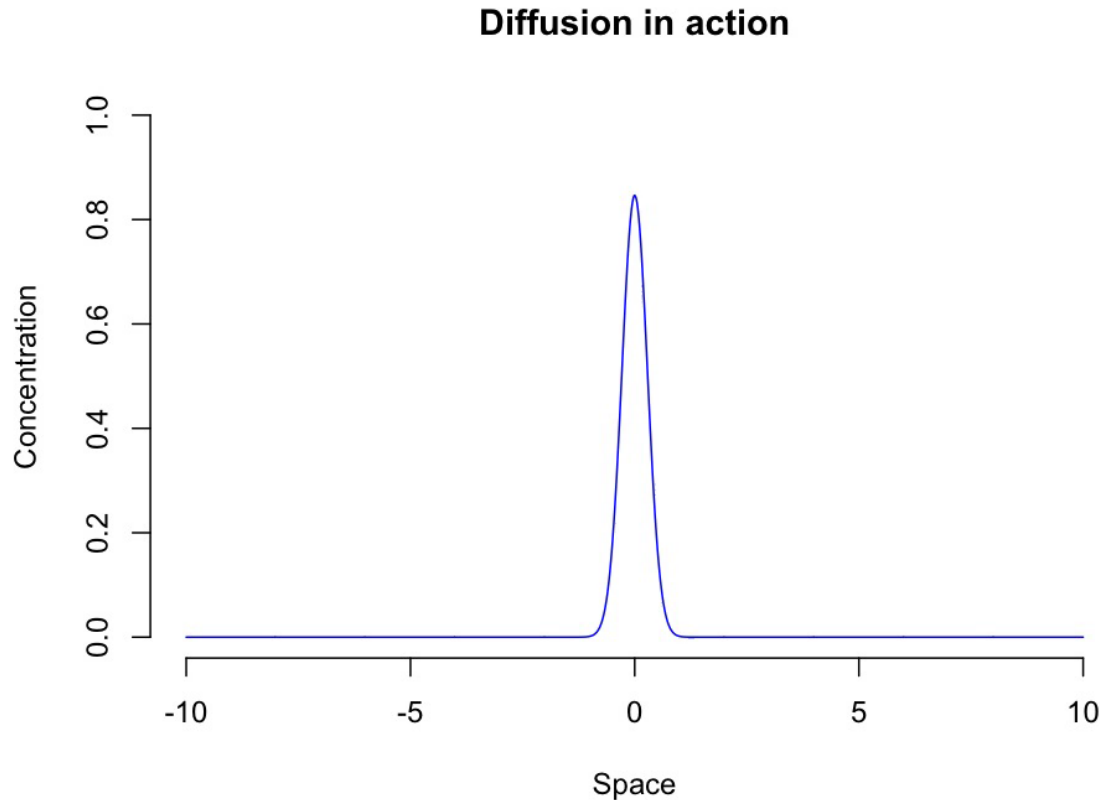
**Growth /
mortality**

**Dispersion
term**

The problem with diffusion

Spatial Ecology

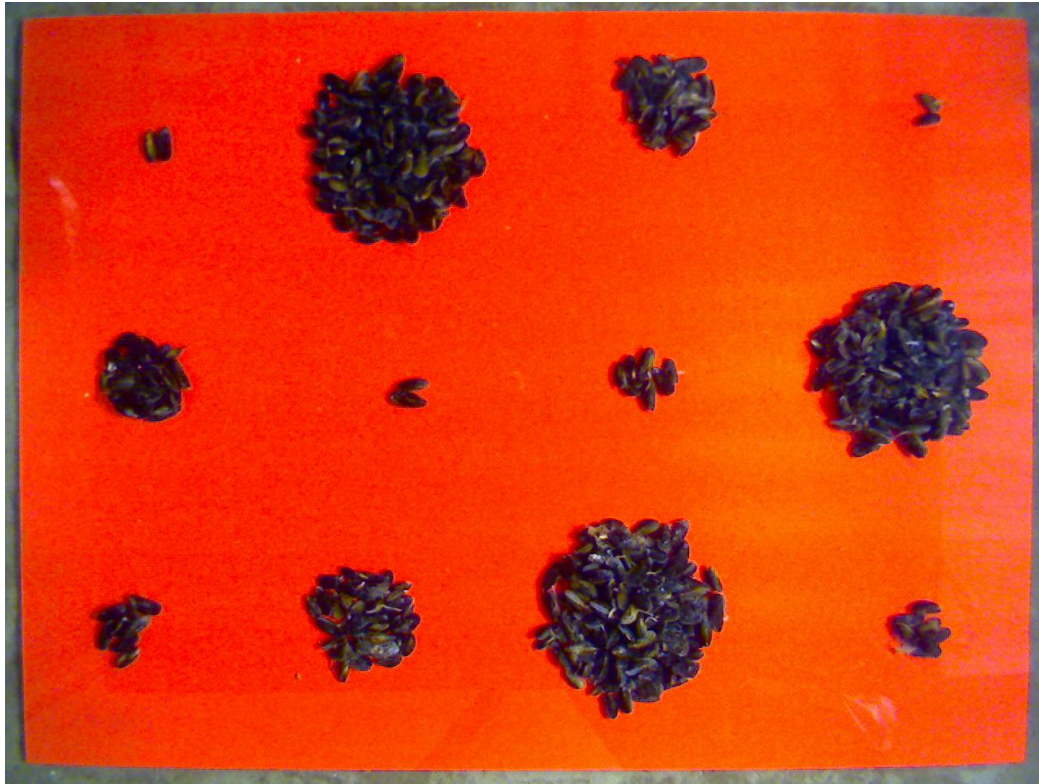
- Diffusive movement only leads to *dispersion* of populations.





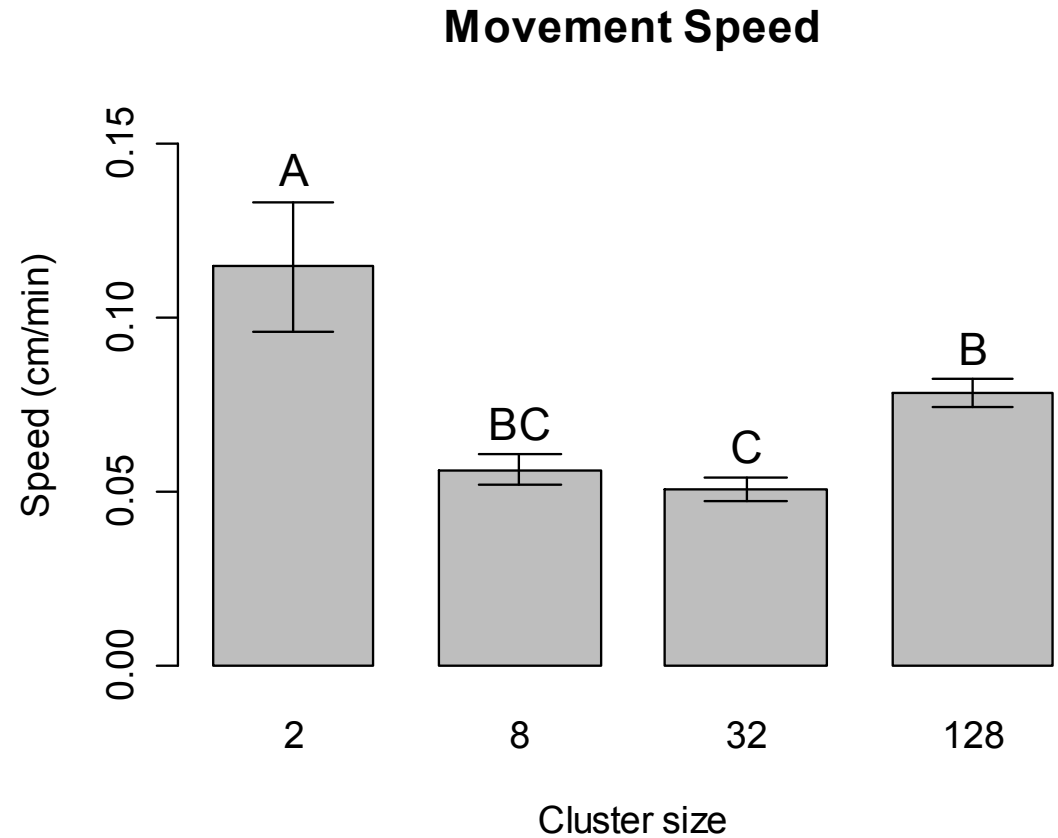
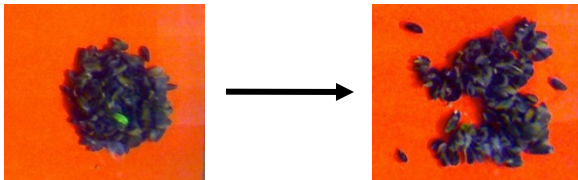
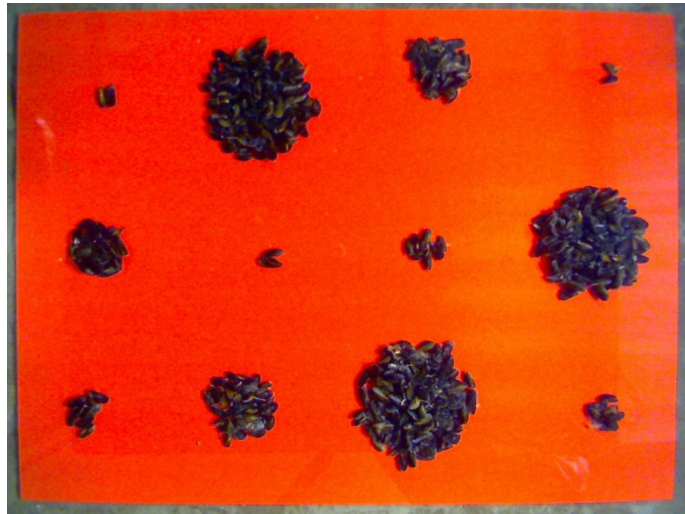
Spatial Ecology

Effect of cluster size on movement



4 cluster sizes:
2, 8, 32 & 128
individuals

Effect of cluster size on movement speed



Density-dependent movement

Spatial Ecology

Classical ecological model

$$\frac{\partial n}{\partial t} = f(n, \dots) + D \frac{\partial^2 n}{\partial x^2}$$

Growth / mortality
Dispersion term

Ecological model with density-dependent movement

$$\frac{\partial n}{\partial t} = f(n, \dots) + D(n, \dots) \frac{\partial^2 n}{\partial x^2}$$

Density-dependent movement

Spatial Ecology

Classical ecological model

$$\frac{\partial n}{\partial t} = f(n, \dots) + D \frac{\partial^2 n}{\partial x^2}$$

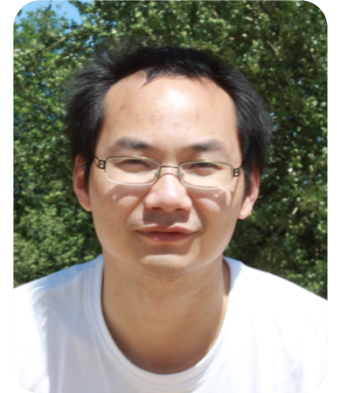
Growth / mortality
Dispersion term

Ecological model with density-dependent movement

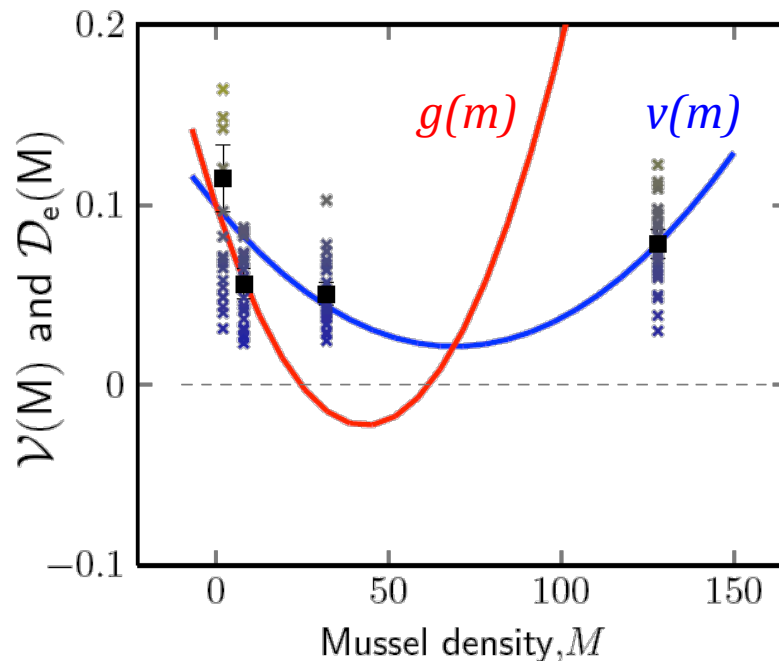
$$\frac{\partial n}{\partial t} = f(n, \dots) + \frac{\partial \left(g(n, \dots) \frac{\partial n}{\partial x} \right)}{\partial x}$$

From individual movement to population dispersion

$$\frac{\partial n}{\partial t} = \underbrace{f(n, \dots)}_{\partial x} + \underbrace{\frac{\partial}{\partial x} \left(g(n) \frac{\partial n}{\partial x} \right)}_{\partial x} + \underbrace{\frac{\partial}{\partial x} \left(g(n, \dots) \frac{\partial n}{\partial x} \right)}_{\partial x}$$



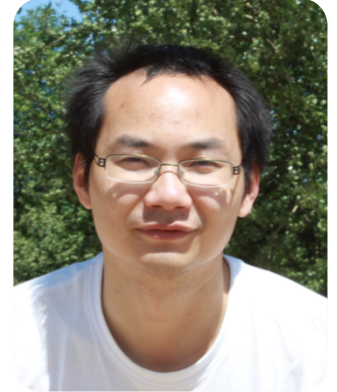
Work of
Quan-Xing Liu



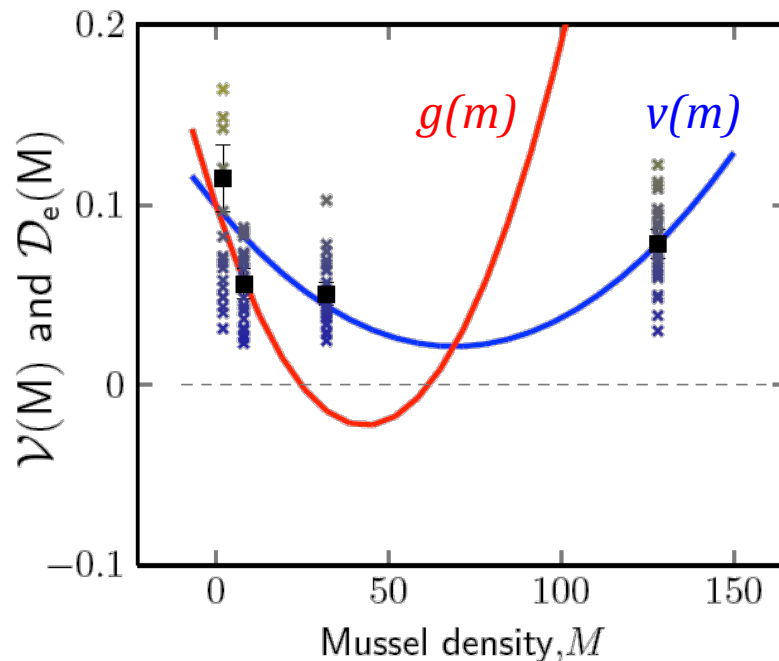
- Use Einstein's theory to translate individual movement v to population dispersion g .
- Include a 4th-order term to avoid over-accumulation.

From individual movement to population dispersion

$$\frac{\partial n}{\partial t} = + \frac{\partial \left(g(n) \frac{\partial n}{\partial x} \right)}{\partial x} - \gamma \frac{\partial^4 n}{\partial x^4}$$



Work of
Quan-Xing Liu



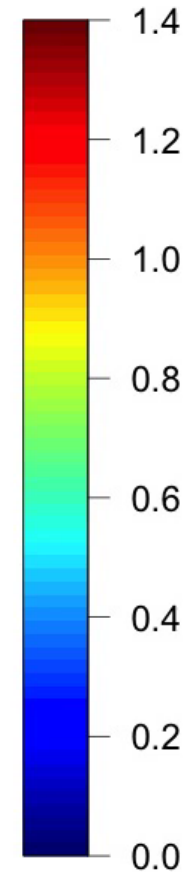
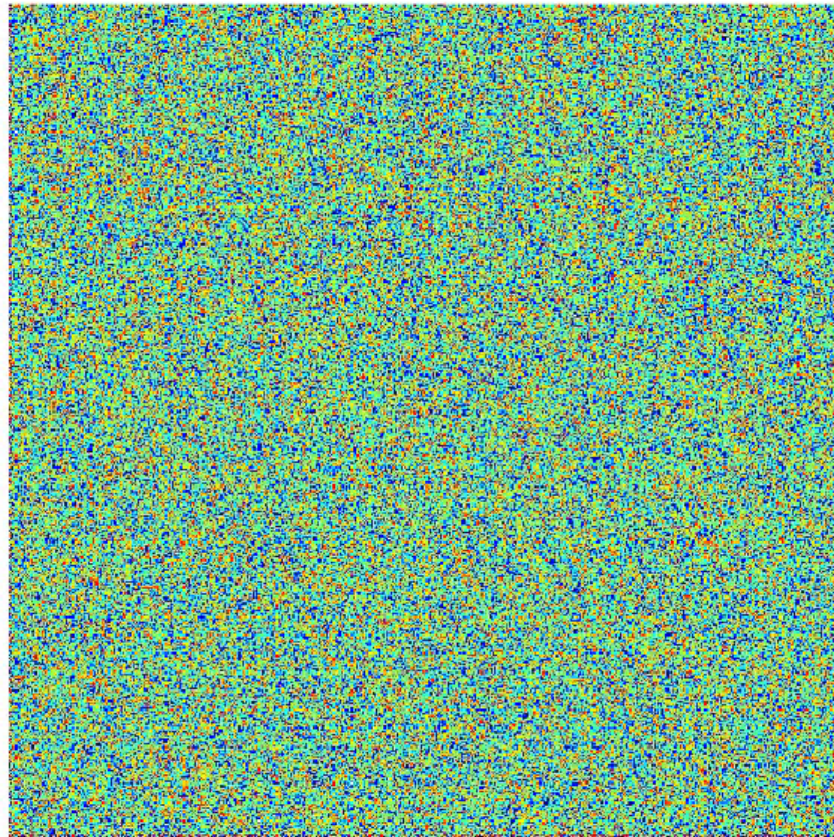
- Use Einstein's theory to translate individual movement v to population dispersion g .
- Include a 4th-order term to avoid over-accumulation.



Spatial Ecology

Mussel pattern formation

Mussel phase separation



Time : 0 of 20000 Minutes

The principle of phase separation

Spatial Ecology



John Cahn

Our model is equivalent to the well-known **Cahn-Hilliard** equation for phase separation:

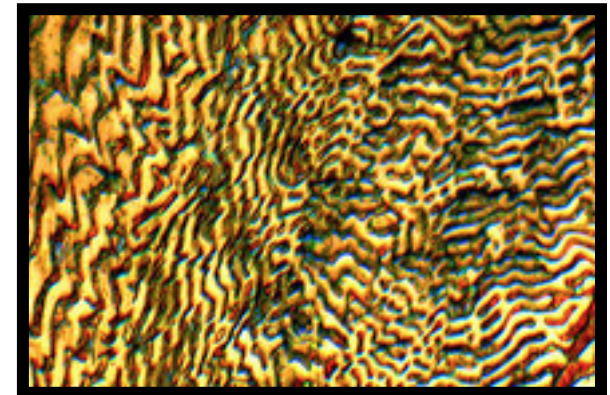
$$\frac{\partial c}{\partial t} = D \nabla^2 (c^3 - c - \gamma \nabla^2 c)$$

=> Used in physics to describe phase separation, for instance in metal alloy formation.

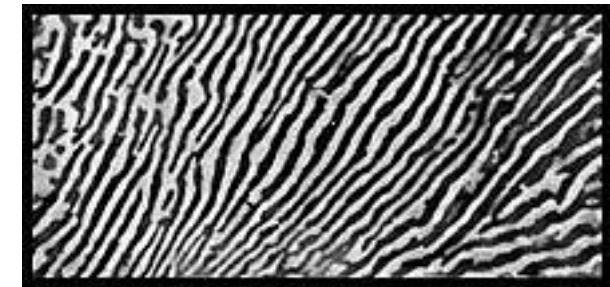
J. W. Cahn and J. E. Hilliard,
J. Chem. Phys. (1958).



John Hilliard



Copper – Phosphorus alloy



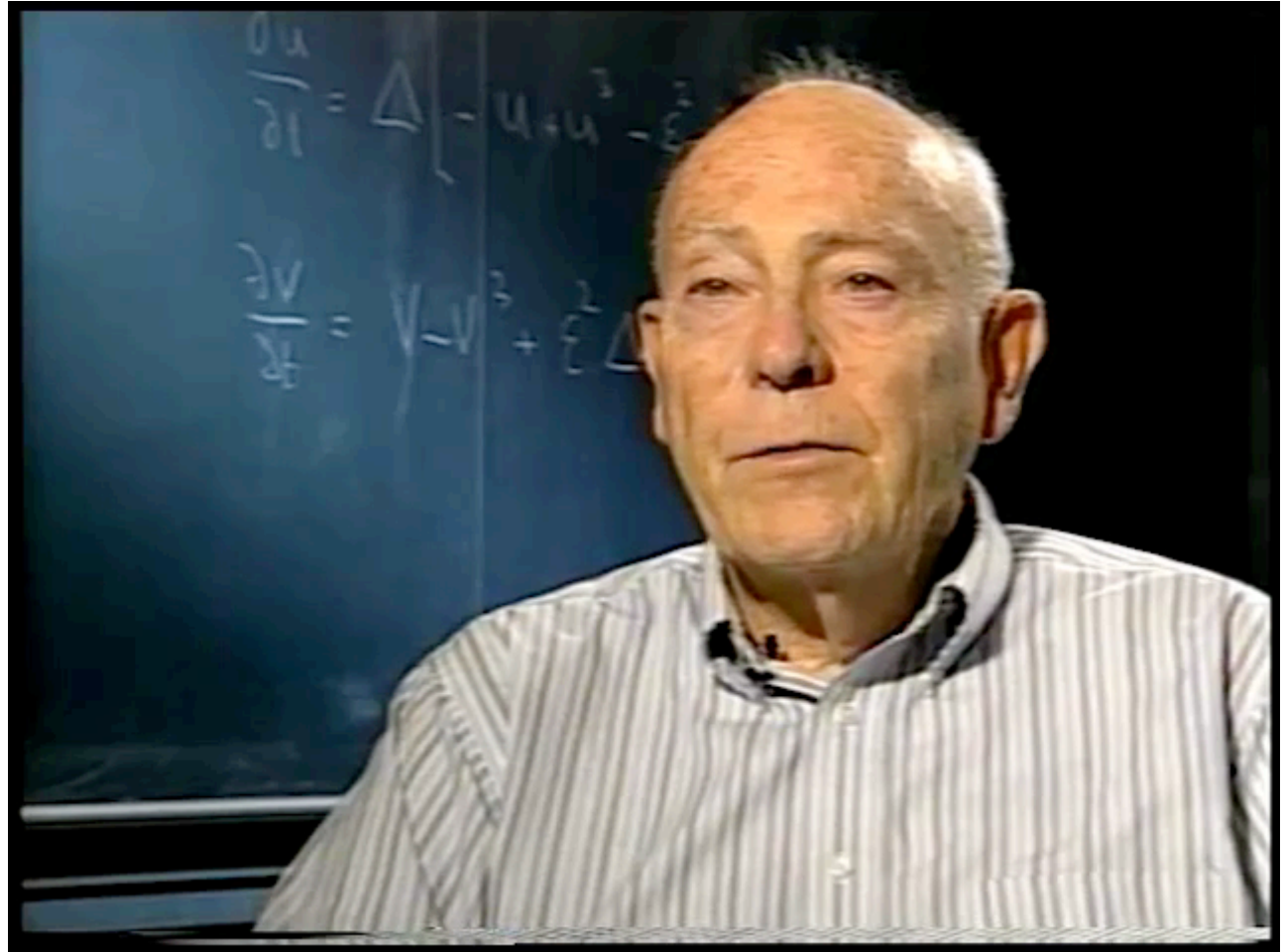
Steel (Iron & Carbon)

John Cahn's view on diffusion

Spatial Ecology



John Cahn
in 1957 (age 29)



For ecologists: when you hear "matter", read: mussels

Movie: John Cahn interviewed in 2001 when receiving the Kyoto prize



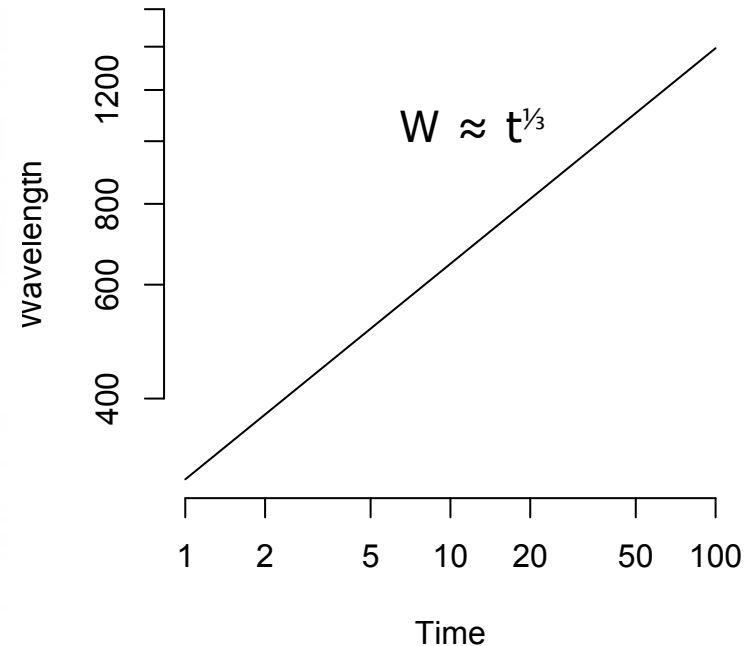
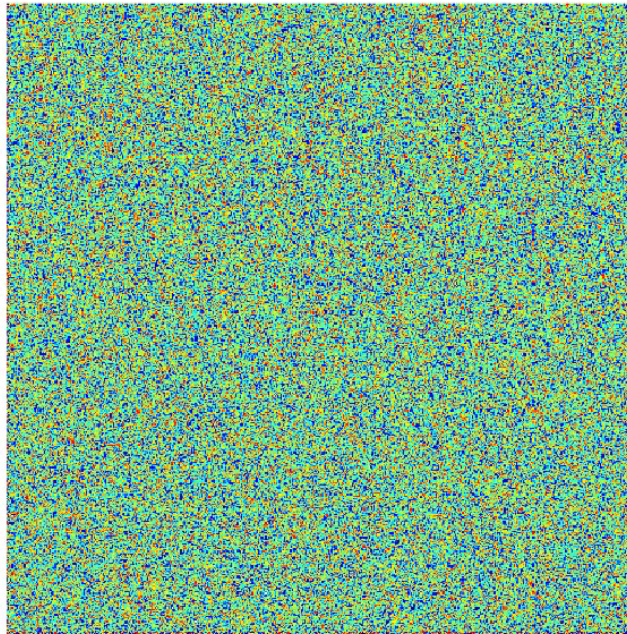
Submitting to a physical audience

Spatial Ecology



Nigel Goldenfeld
Department of Physics
University of Illinois

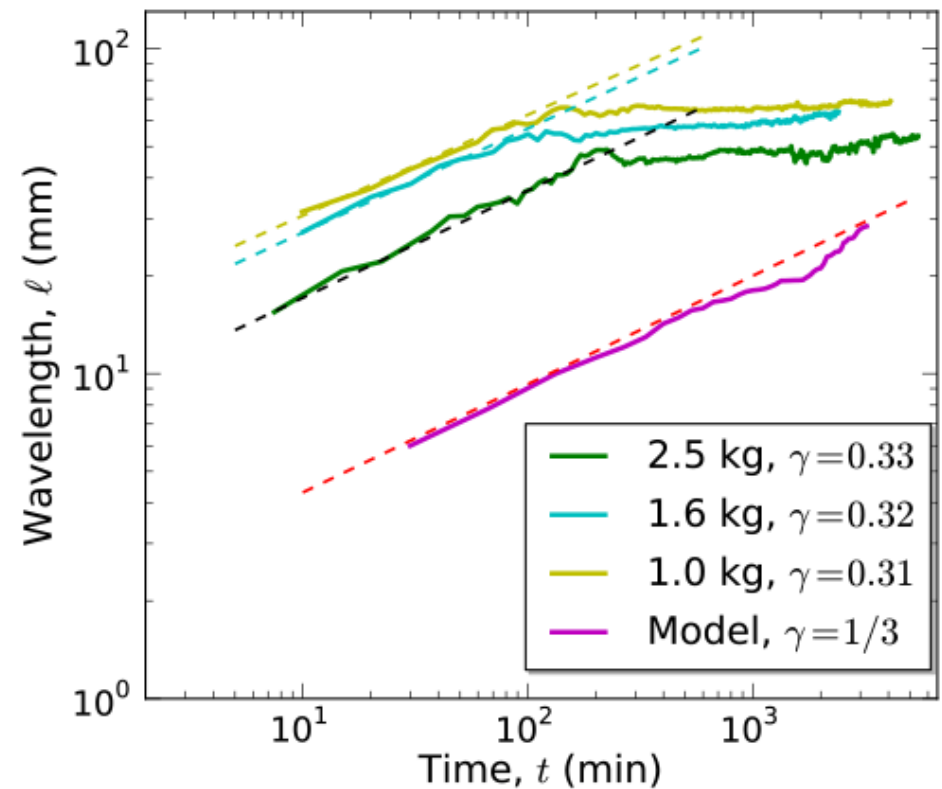
- Reviewer Nigel Goldenfeld (physicist):
I don't believe this if the coarsening doesn't follow the Lifshitz–Slyozov law.



Coarsening & the Lifshitz–Slyozov law

Spatial Ecology

- Do patterns in mussel beds coarsen in time?

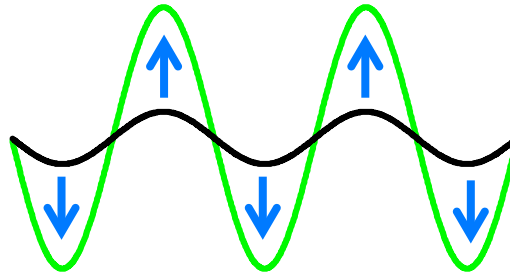


Two fundamental principles of pattern formation



Turing 1952

Type 1: Growth-driven self-organization
(**Activator-inhibitor** principle)

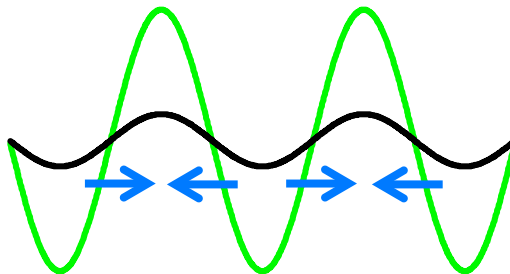


Arid vegetation patterns



John Cahn 1957

Type 2: Movement-driven self-organization
(**Phase separation** principle)

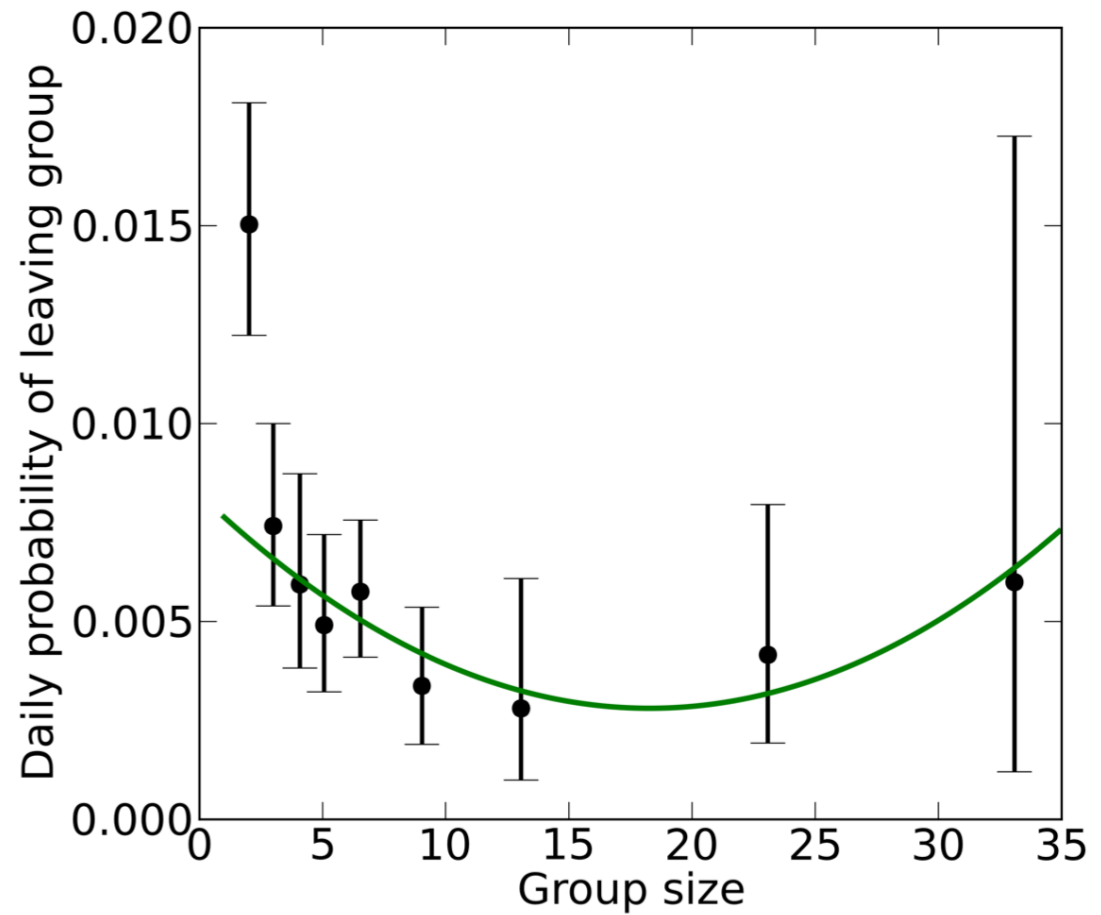


Mussel clump patterns

Liu et al, PNAS 2013

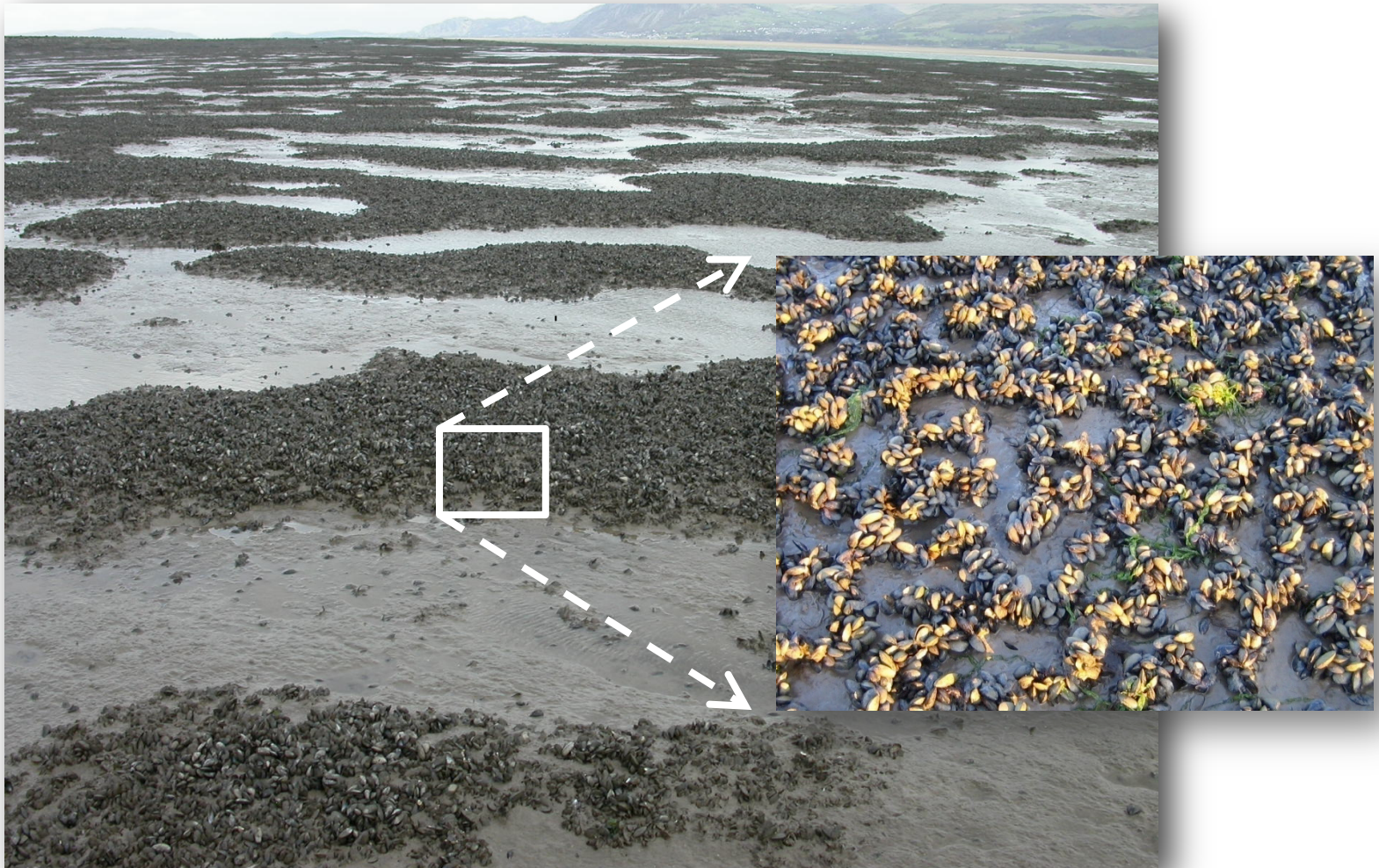


Only mussels?



Aggregation at two scales

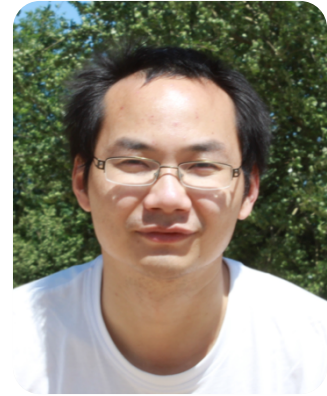
Is this relevant?



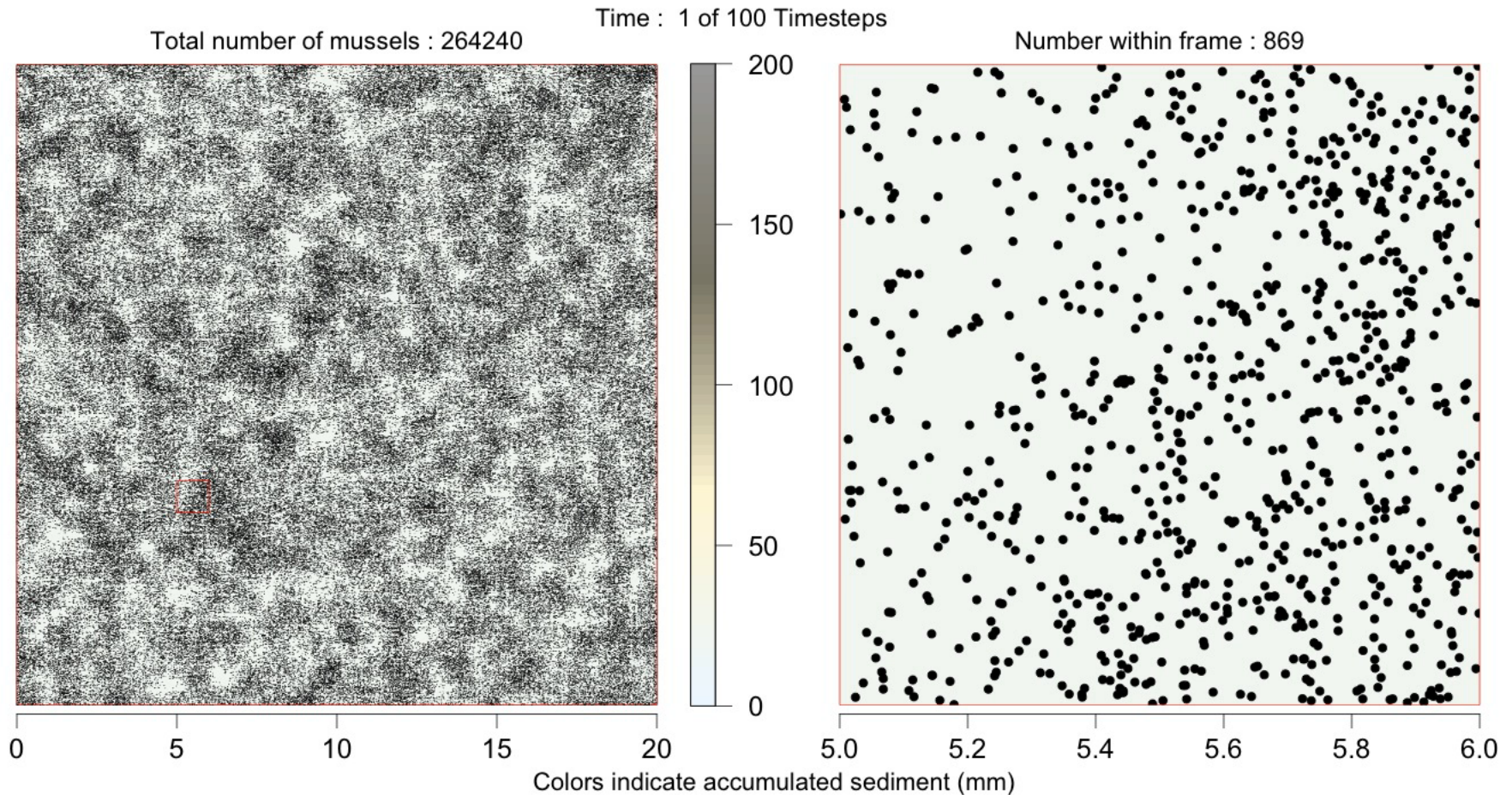


A big model!

Spatial Ecology



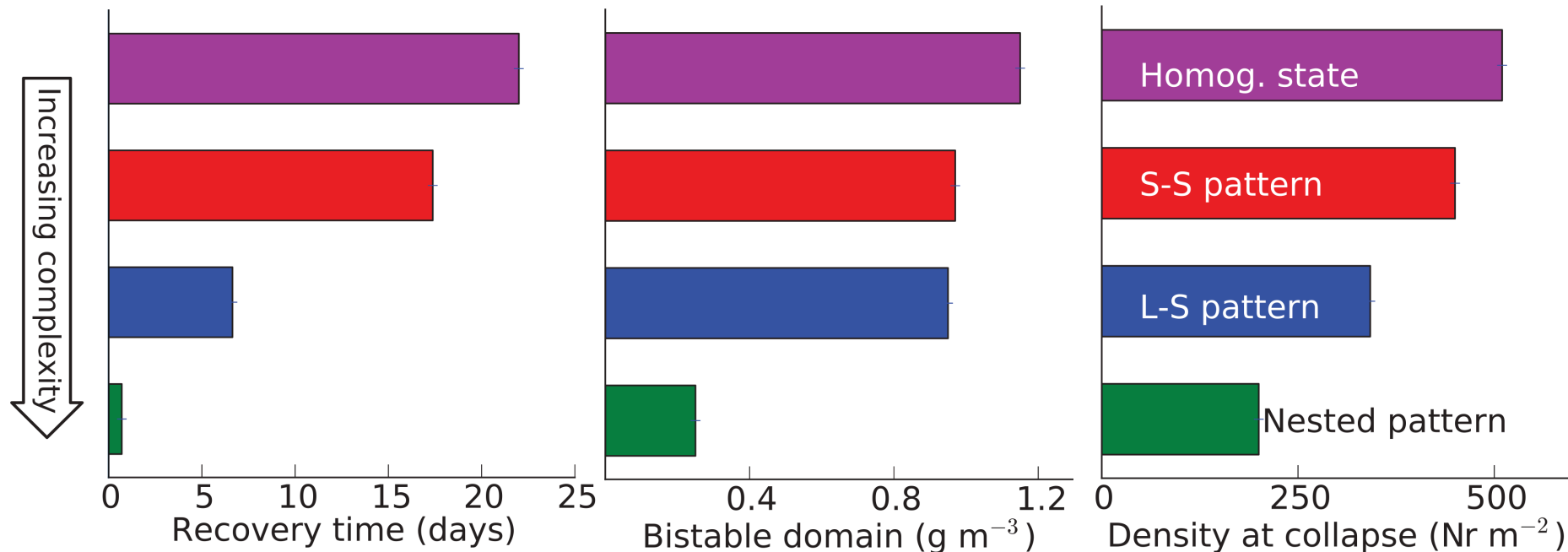
Work of Quan-Xing Liu



Do patterns matter?

Spatial Ecology

What models say:



And now for real!



Natuurmonumenten



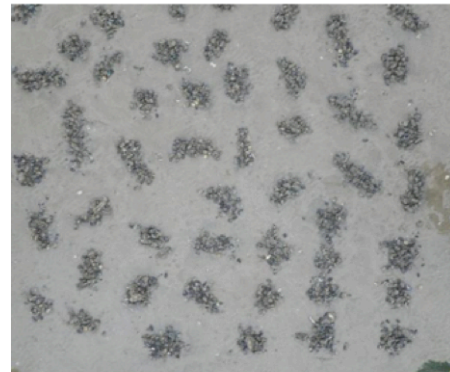
Testing the effects of aggregation at two spatial scales

Spatial Ecology

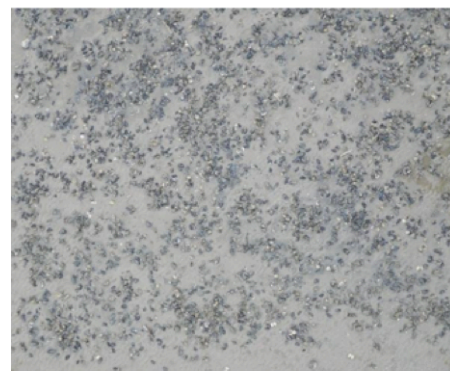
Bands

No Bands

Clumps



No
Clumps



Hélène
de Paoli



WADDEN
sleutels

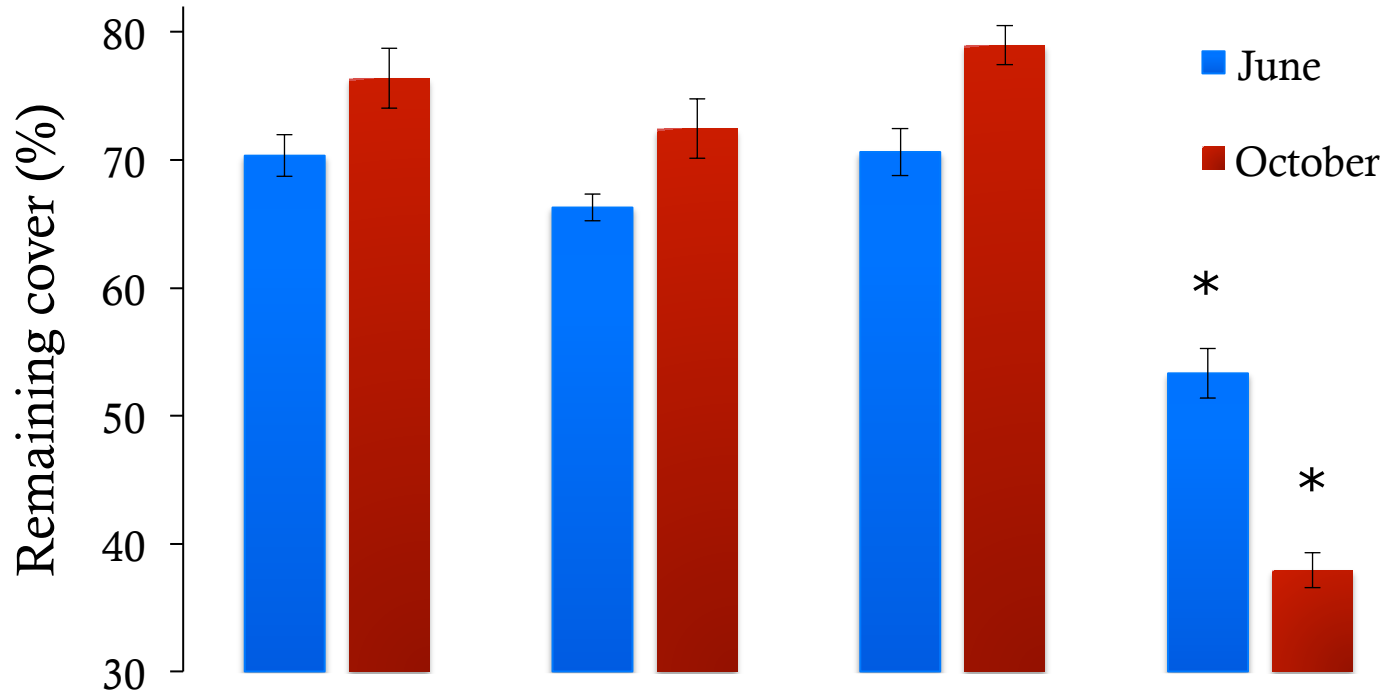


Do patterns matter?

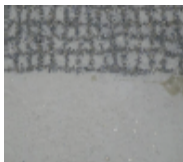
Spatial Ecology



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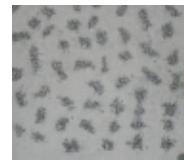
Bands
Attached



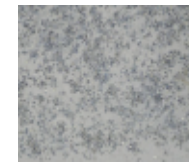
Bands
Non attached



No bands
Attached



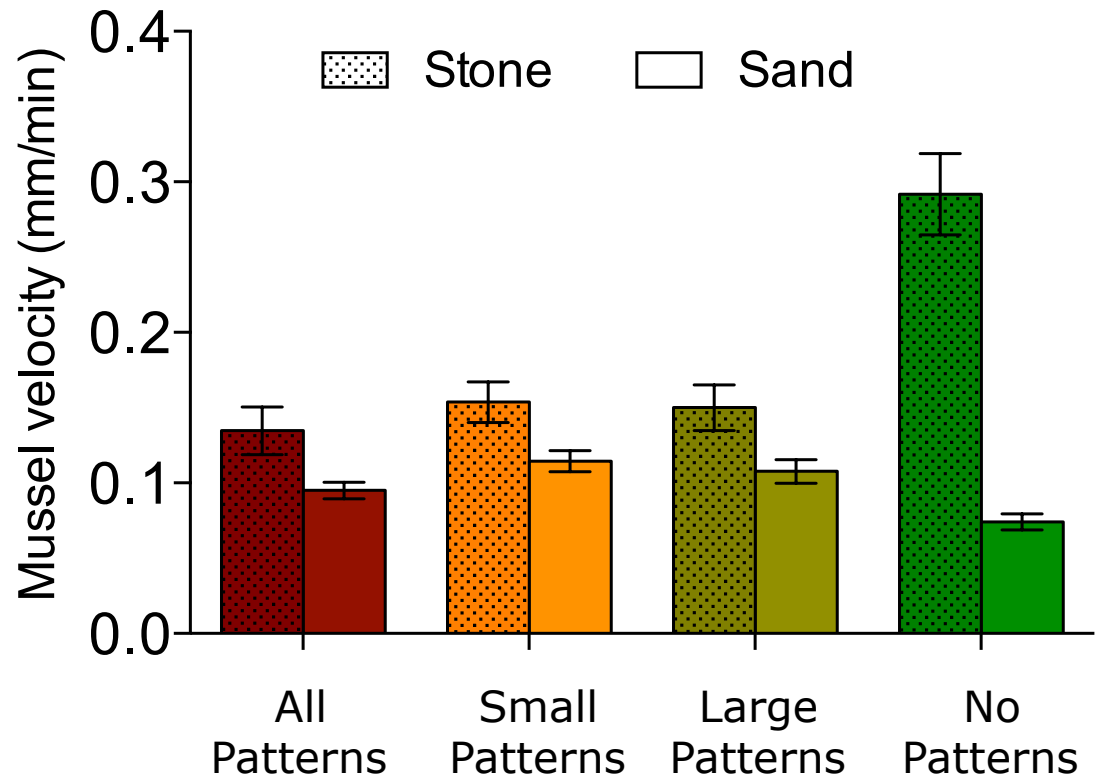
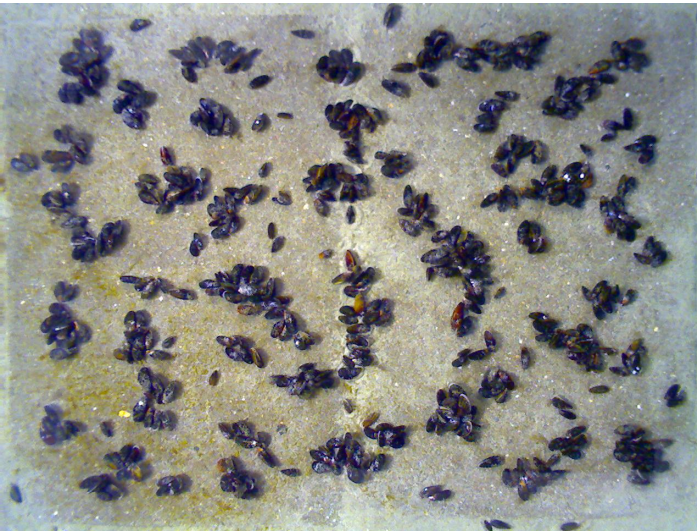
No bands
Non attached



WADDEN
sleutels



The ultimate cause: Phase separation failure!





Spatial Ecology

A multidisciplinary approach

Physical principles applied to pattern formation in organisms:

- Levy walks (adaptive in patterns)
- Collisions explain Brownian motion (Einstein)
- Phase separation drives pattern formation (Cahn)

Crucial to explain:

- Ecosystem persistence
- Organism adaptation

