Foraging behaviour in small organisms

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NMA course, Bergen 2005

Solving foraging problems without a brain?

- Many cells have motility, e.g. flagella and cilia
- Many “aneural” can perceive chemical cues (and other cues) and elicit motor repsonses

Why do microbes move?

Is space that heterogeneous? Yes, probably

And do they move non-randomly?

Do they show adaptive behaviour?

Why move with less than mm/s?

- Foraging
- Predator avoidance
- Mate search
- Avoidance of abiotic stress

Consequences of microbial movement

- Predator - prey interactions (encounter rates)
- Biomass turnover >> rates of biogeochemical cycling

How to aggregate in favourable locations?

Focus on how small organisms may exploit food patches

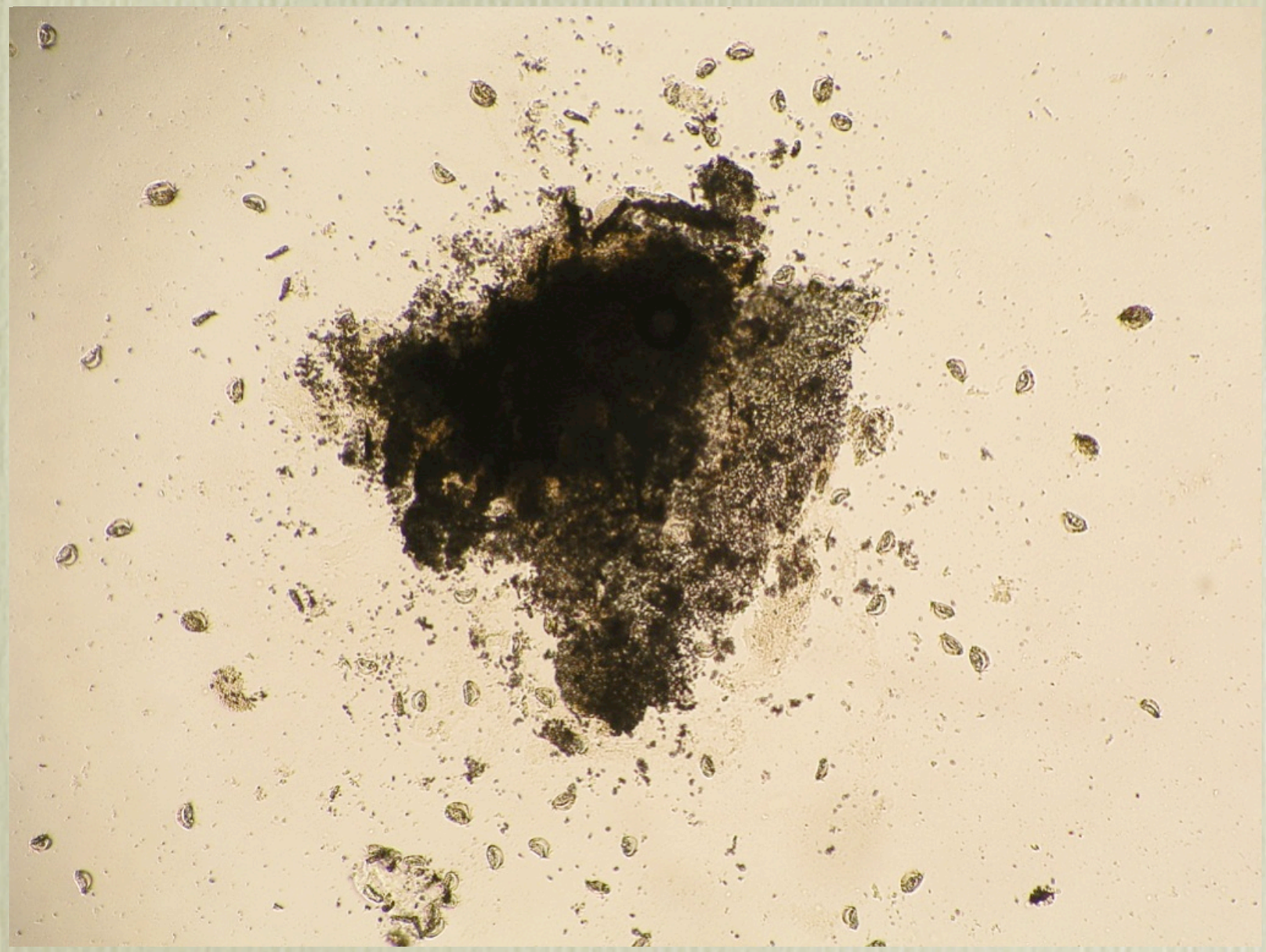
- Find food patches
- Stay in food patches
- Leave patches when food is depleted

The problem

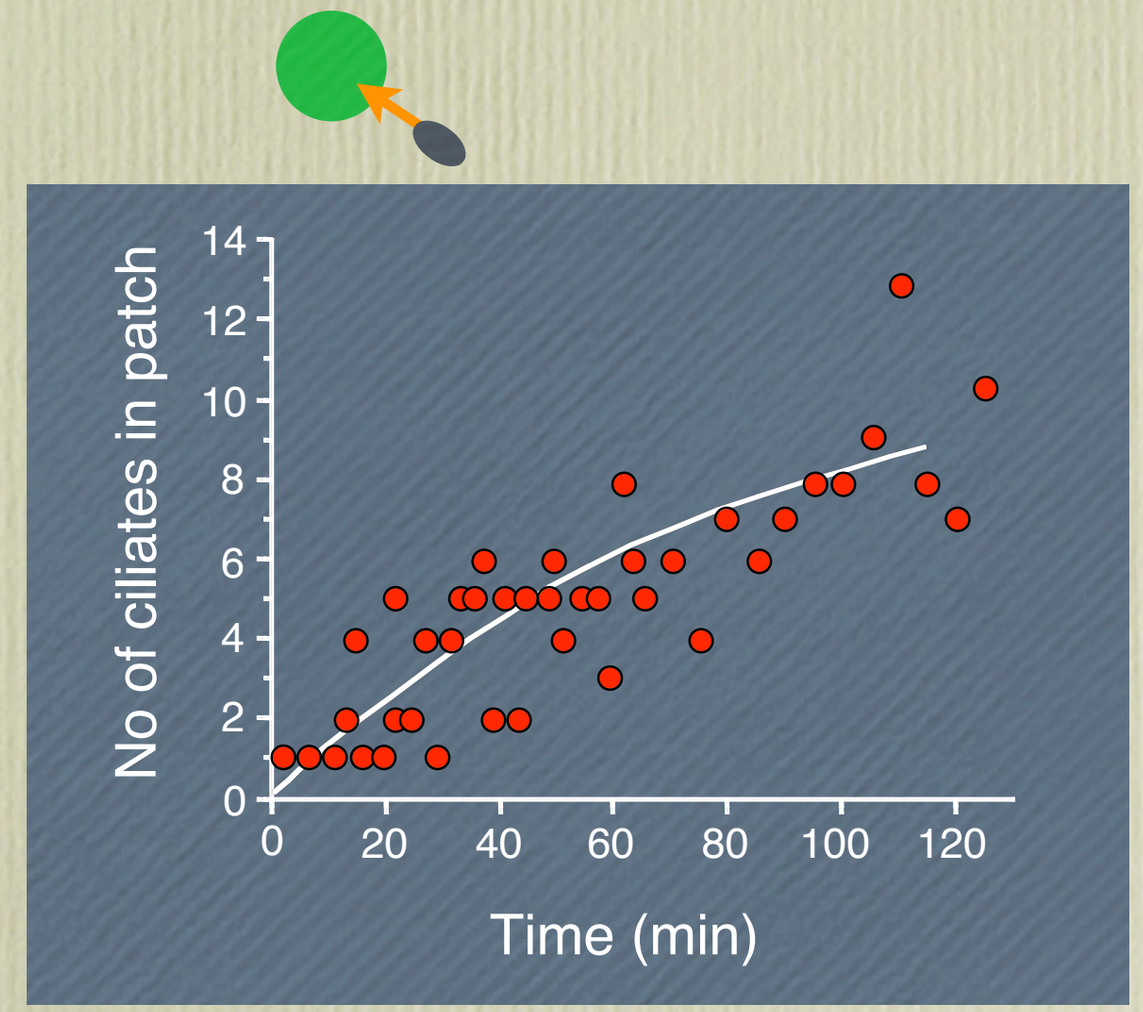
Example: epibenthic ciliates

Euplotes sp.

Aggregation in food patch



What is making *Euplotes* accumulate?



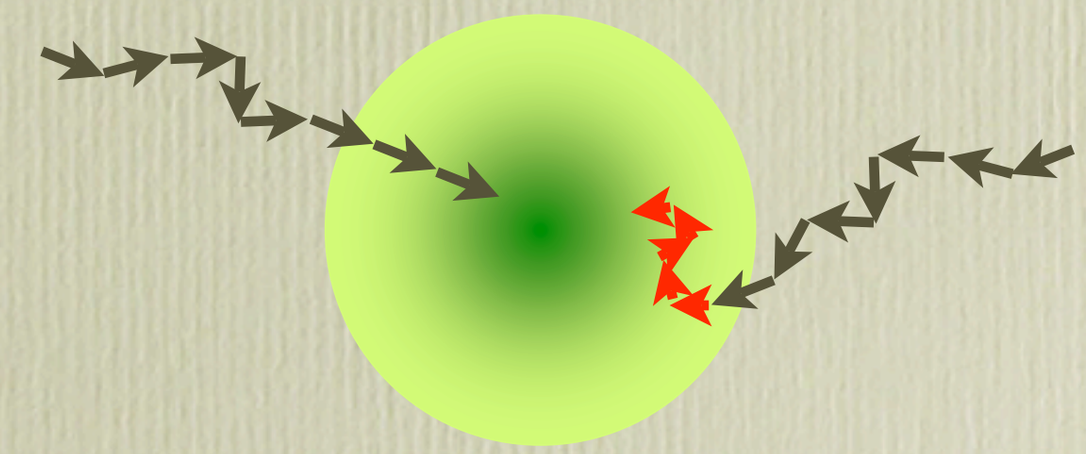
Jonsson & Johansson 1997

Accumulation with time

Taxis or kinesis?

(Taxis is the movement in the direction of a stimulus gradient)

Kinesis is a change in movement in response to the intensity of the stimulus

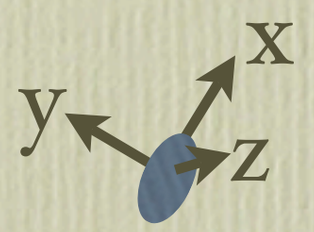


Analysis of aggregation by modelling movement

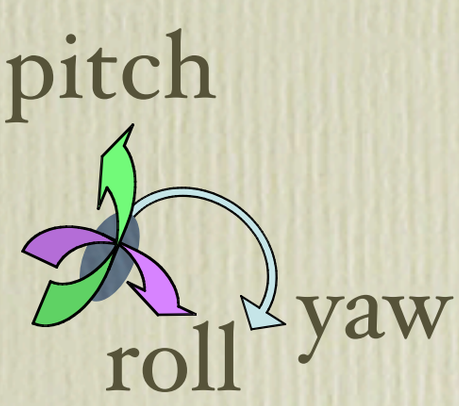
- Define parameters that can describe movement patterns
- What movement patterns may lead to aggregation?

Motion degrees of freedom

- 3 translational degrees of freedom
- 3 rotational degrees of freedom



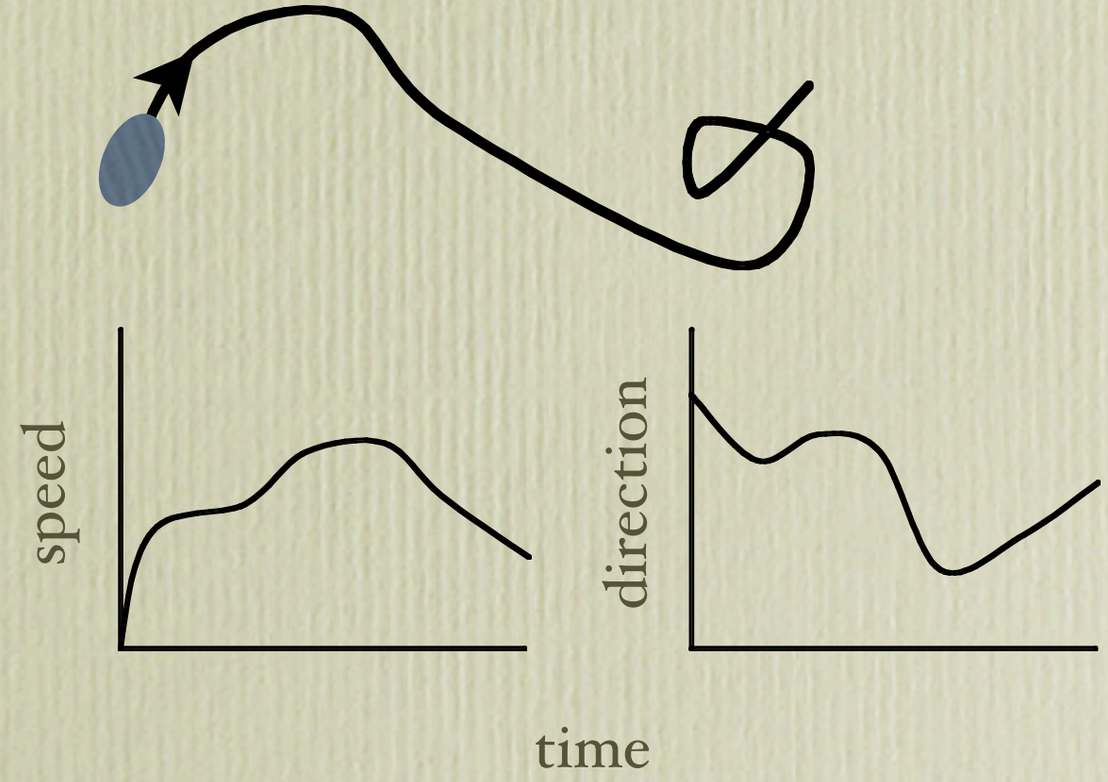
translation



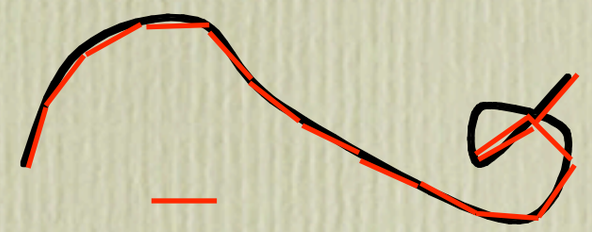
rotation

Fundamental components of movements

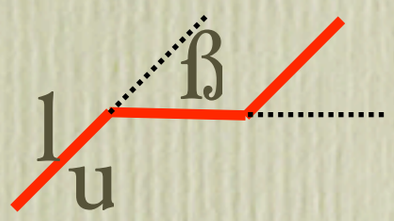
- Velocity as a function of time



Discretization of paths



step length

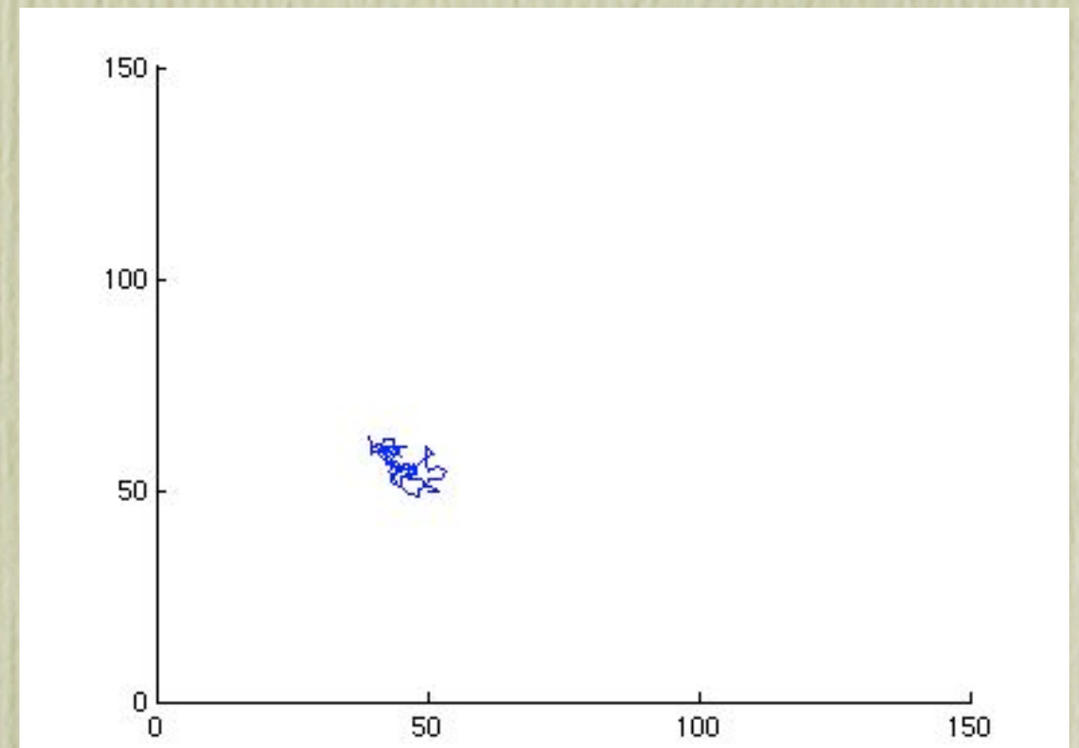


u = speed

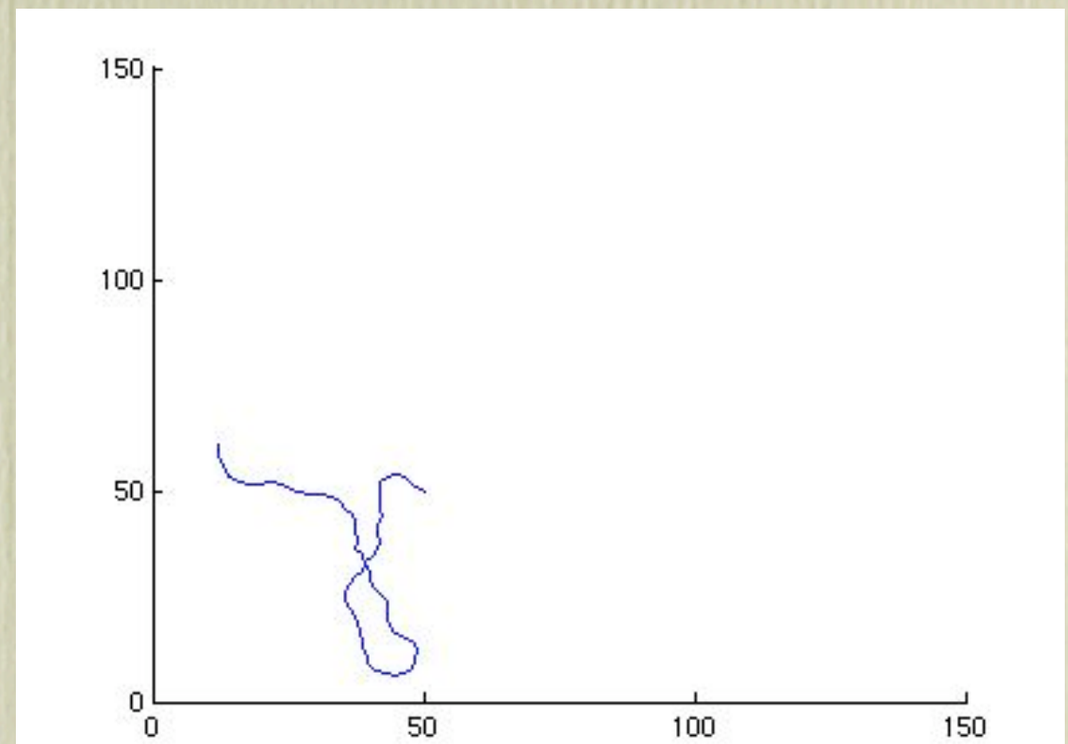
l = step length

ß = angle of direction change

Random walks

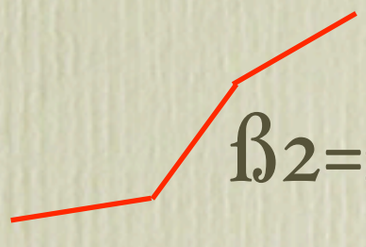


uncorrelated



correlated

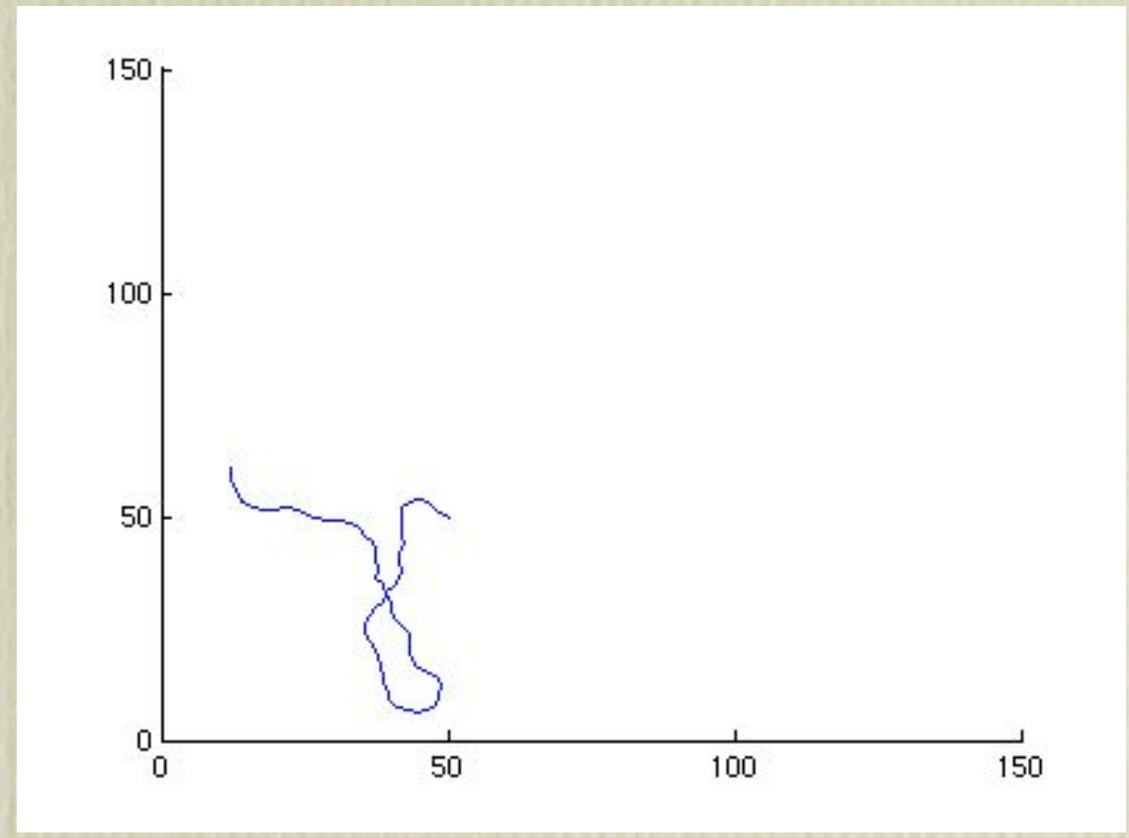
ß=±π*rand



ß2=±<π*rand+ß1

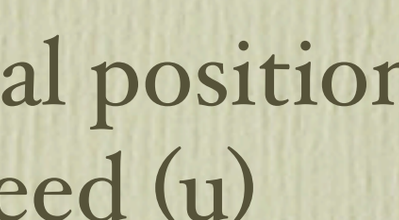
Analysis of movement

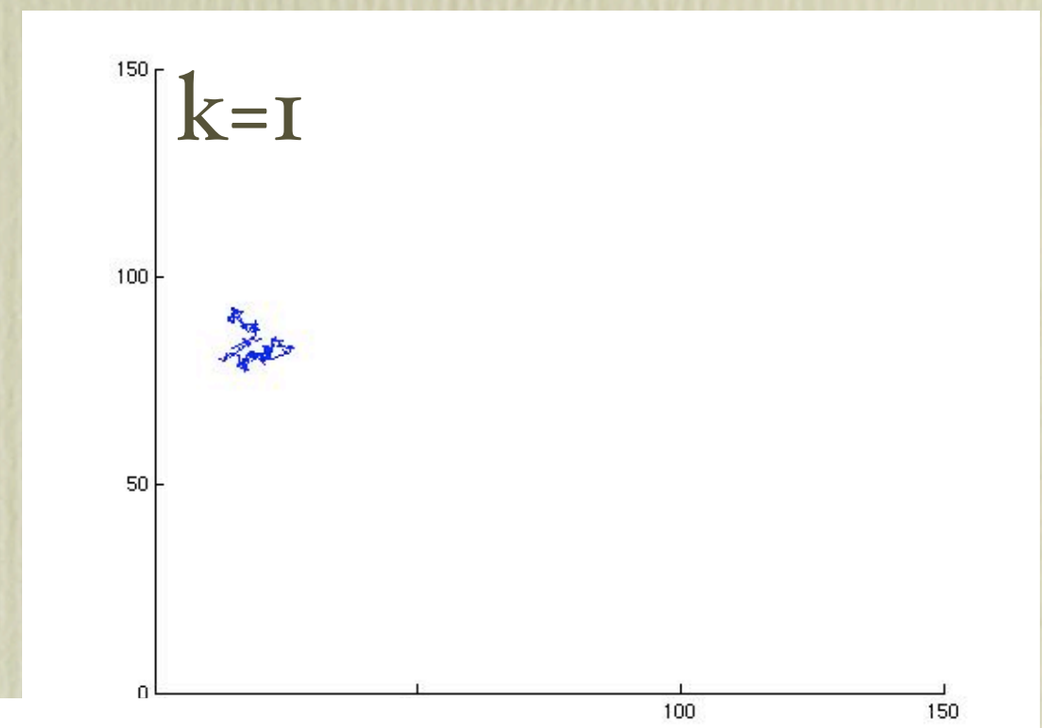
- Primary parameters describing path
  - speed
  - frequency of direction changes
  - angular correlation
- Secondary parameters
  - sinousity
  - diffusion constant
  - fractal dimension

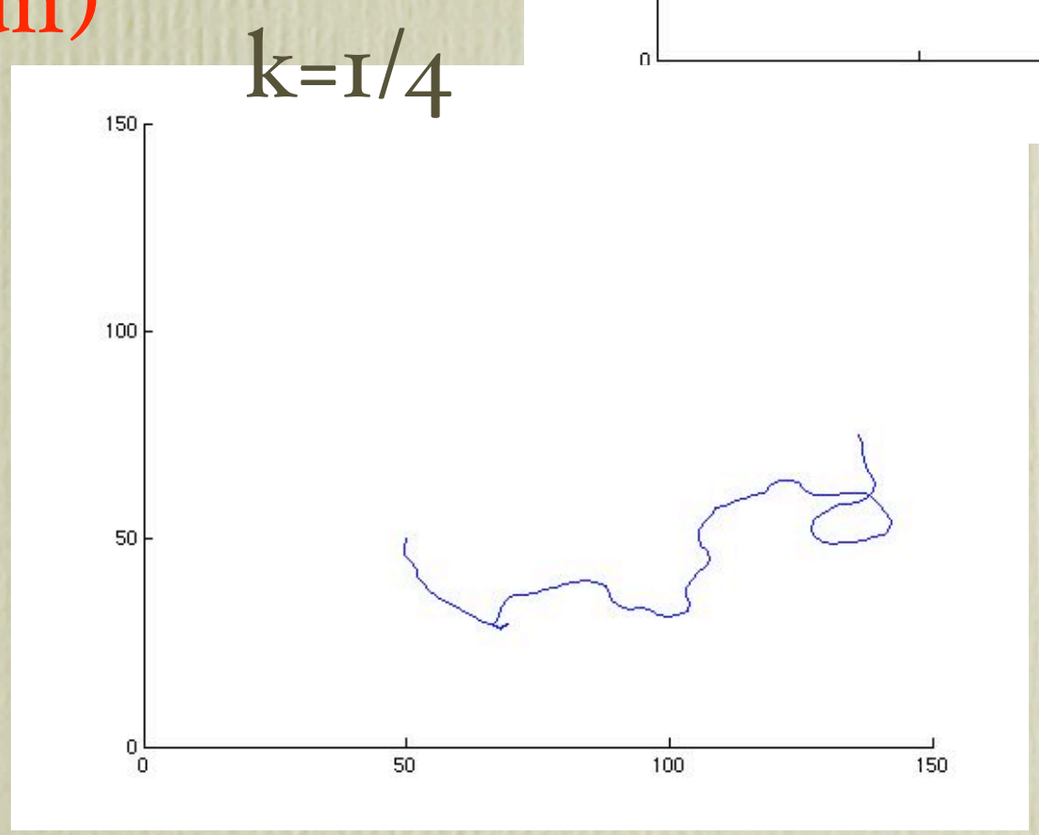


Simulation of ciliate movement

select initial position (x(1), y(1))
select a speed (u)
  for t=2 to 100
    dir=k*2π*(rand-0.5)+dir
    x(t)=x(t-1)+u*sin(dir)
    y(t)=y(t-1)+u*cos(dir)
  next t
plot(x,y)



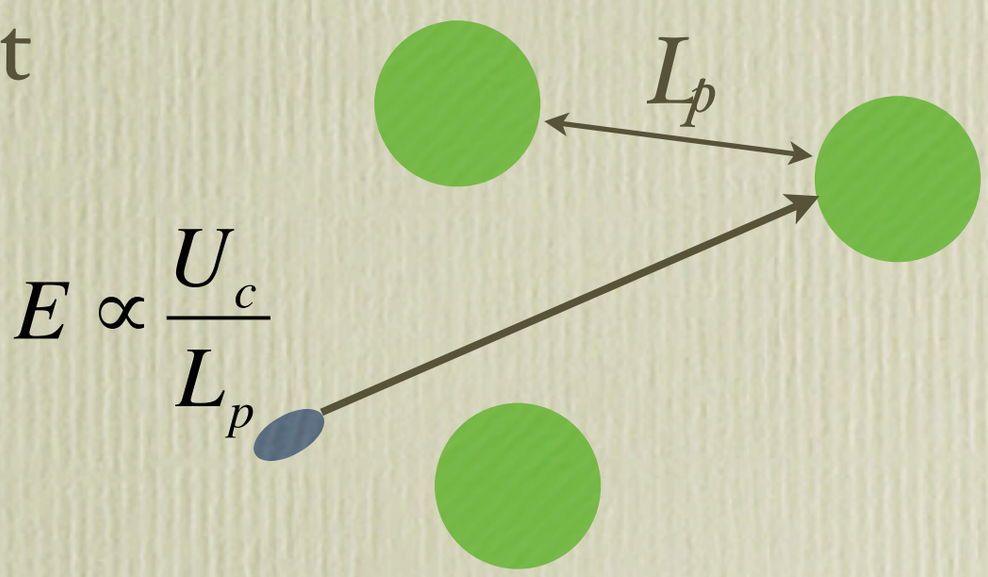




How to find a patch?

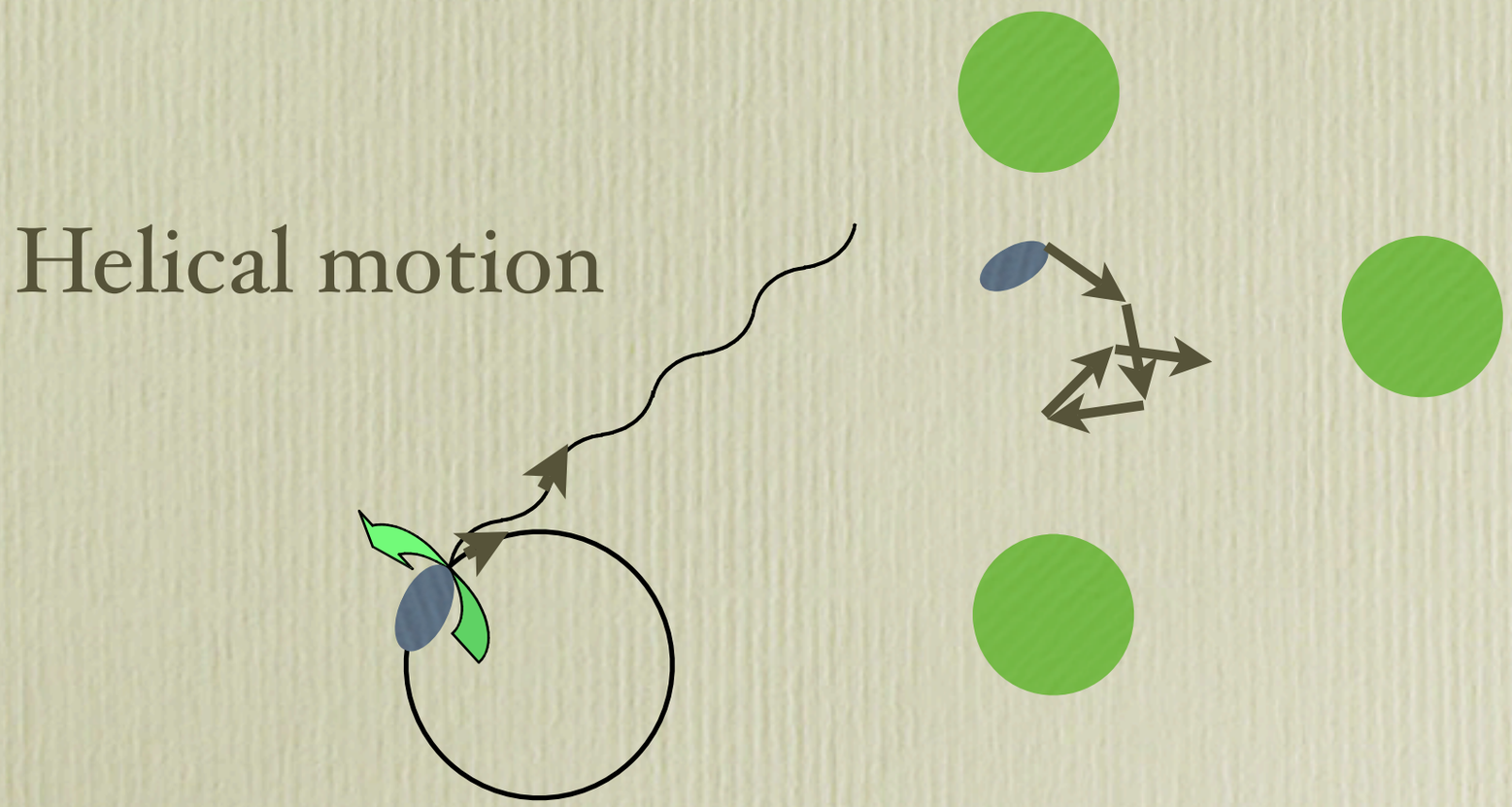
- an encounter problem

- How to search for patches if they cannot be detected from a distance?
- Ballistic movement



Constraint for small organisms

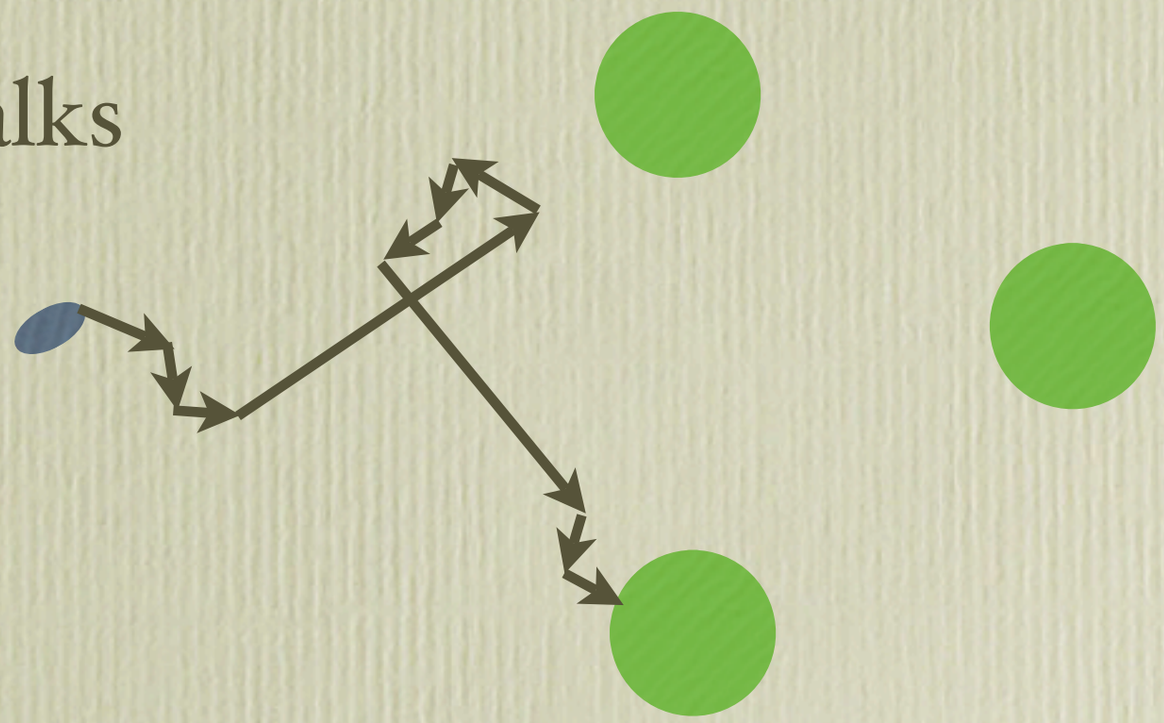
Difficult to move in ballistic paths



Helical motion

Constraint for small organisms

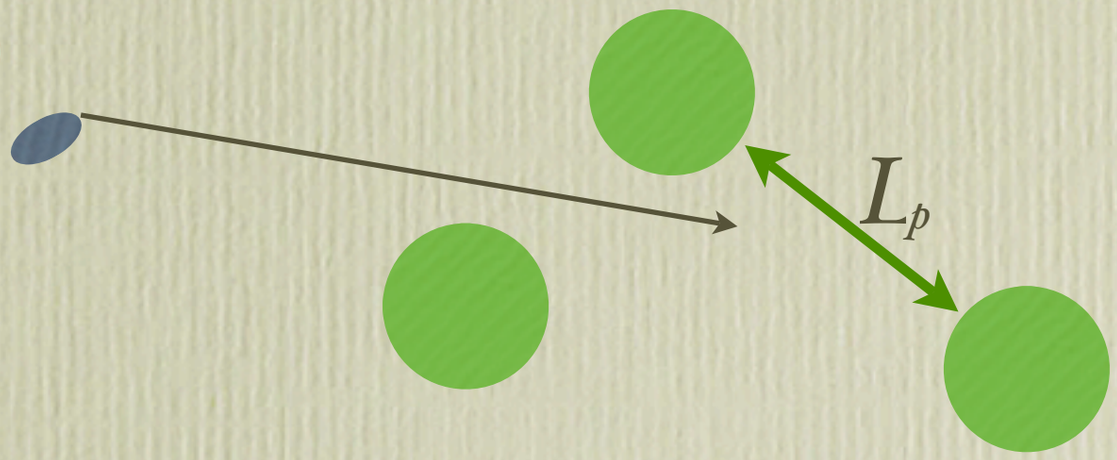
- Minimize crossing the path
- Levy walks



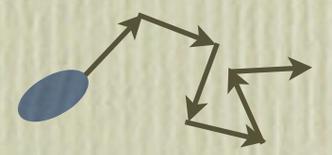
Encounter rate with patches

- summary

$$E \propto \frac{U_c}{L_p}$$



$$E \propto \frac{4D_c}{L_p^2}$$



$$D_c = \frac{\left(1+\overline{\cos(\beta)}\right)U_c l}{4\left(1-\overline{\cos(\beta)}\right)}$$

How fast is patch encounter for a random-walk ciliate?

Typical diffusion constant = 5 mm^2 /s

$$E \propto \frac{4D_c}{L_p^2} \quad D_c = \frac{\left(1+\overline{\cos(\beta)}\right)U_c l}{4\left(1-\overline{\cos(\beta)}\right)}$$

- Patch distance 1 cm, time to encounter ≈ 10 s
- Patch distance 10 cm, time to encounter ≈ 9 min
- Patch distance 1 m, time to encounter ≈ 14 h

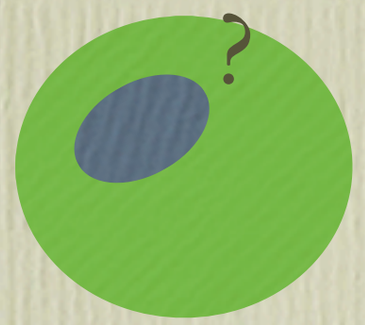
Ciliate motility can only exploit small-scale patchiness!

Speculations

- Cues unrelated to food may be used to make movement more ballistic
  - Light
  - Gravity

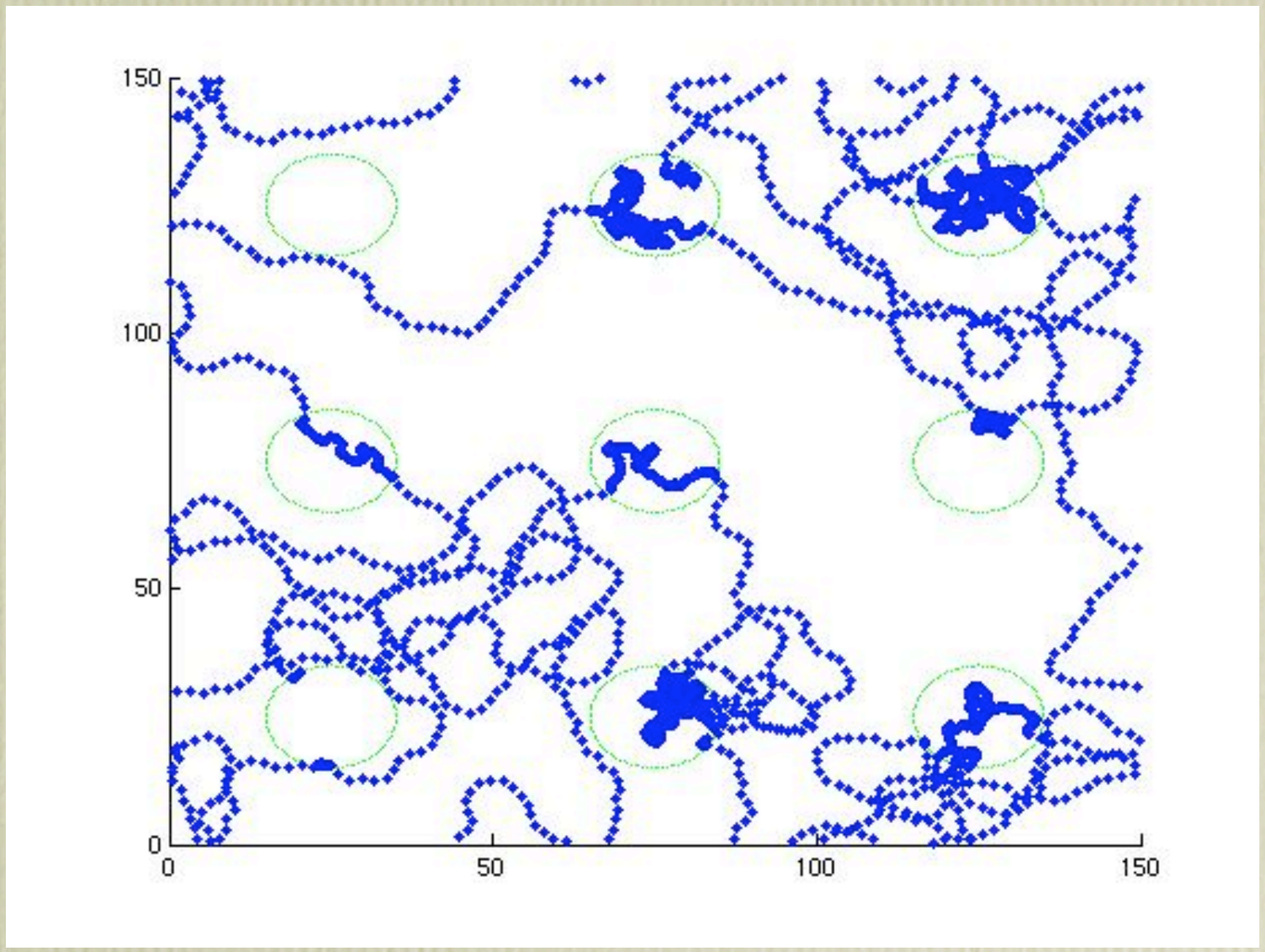
How does a ciliate stay in a patch?

Response to aboslute concentration



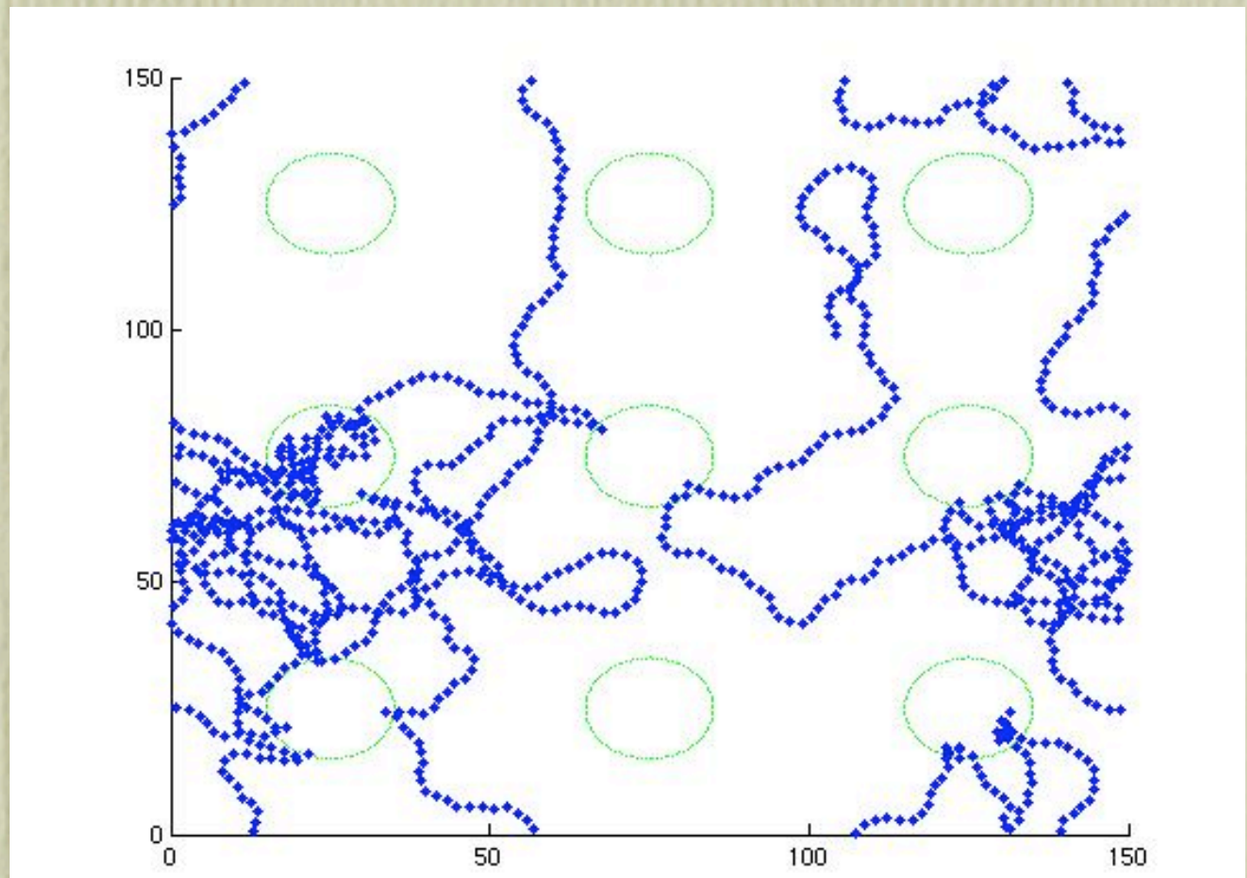
Slow down in patch

45% of time spent in patches compared to 12% with no response

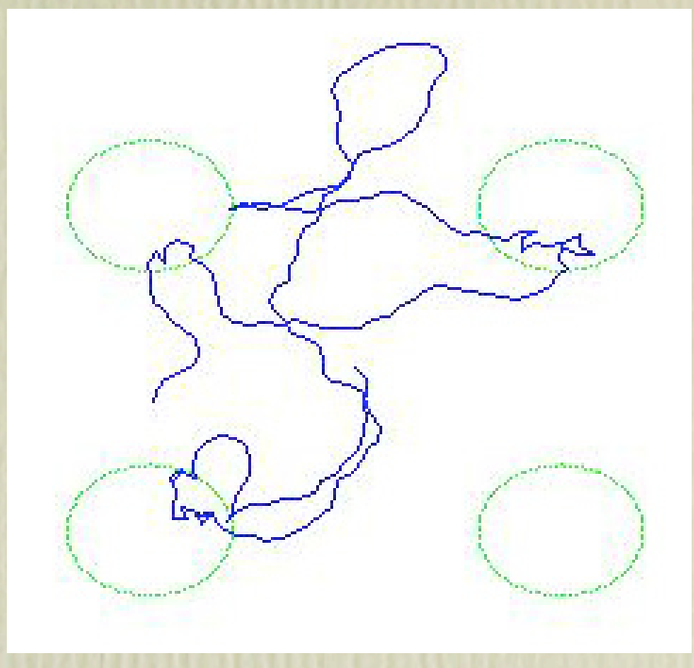


Reduced velocity in food patch: orthokinesis

Increase change of direction in patch

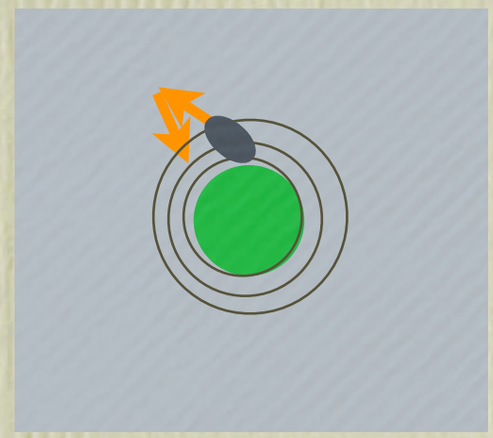


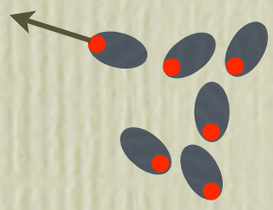
Change of turning frequency in food patch: klinokinesis



No effect on patch time

Response to gradients

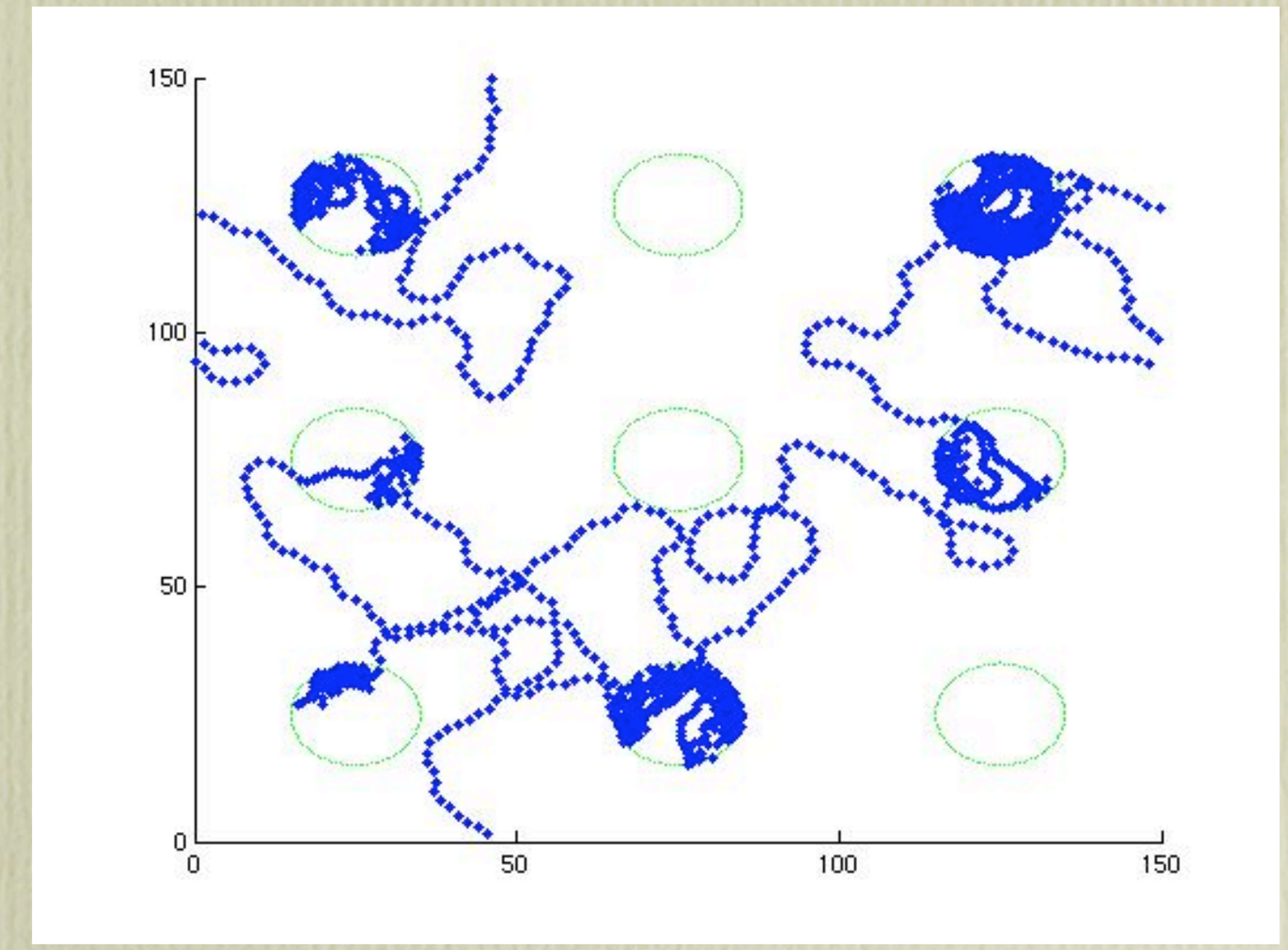




Tumble

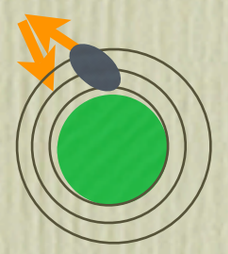
Model of response to gradients

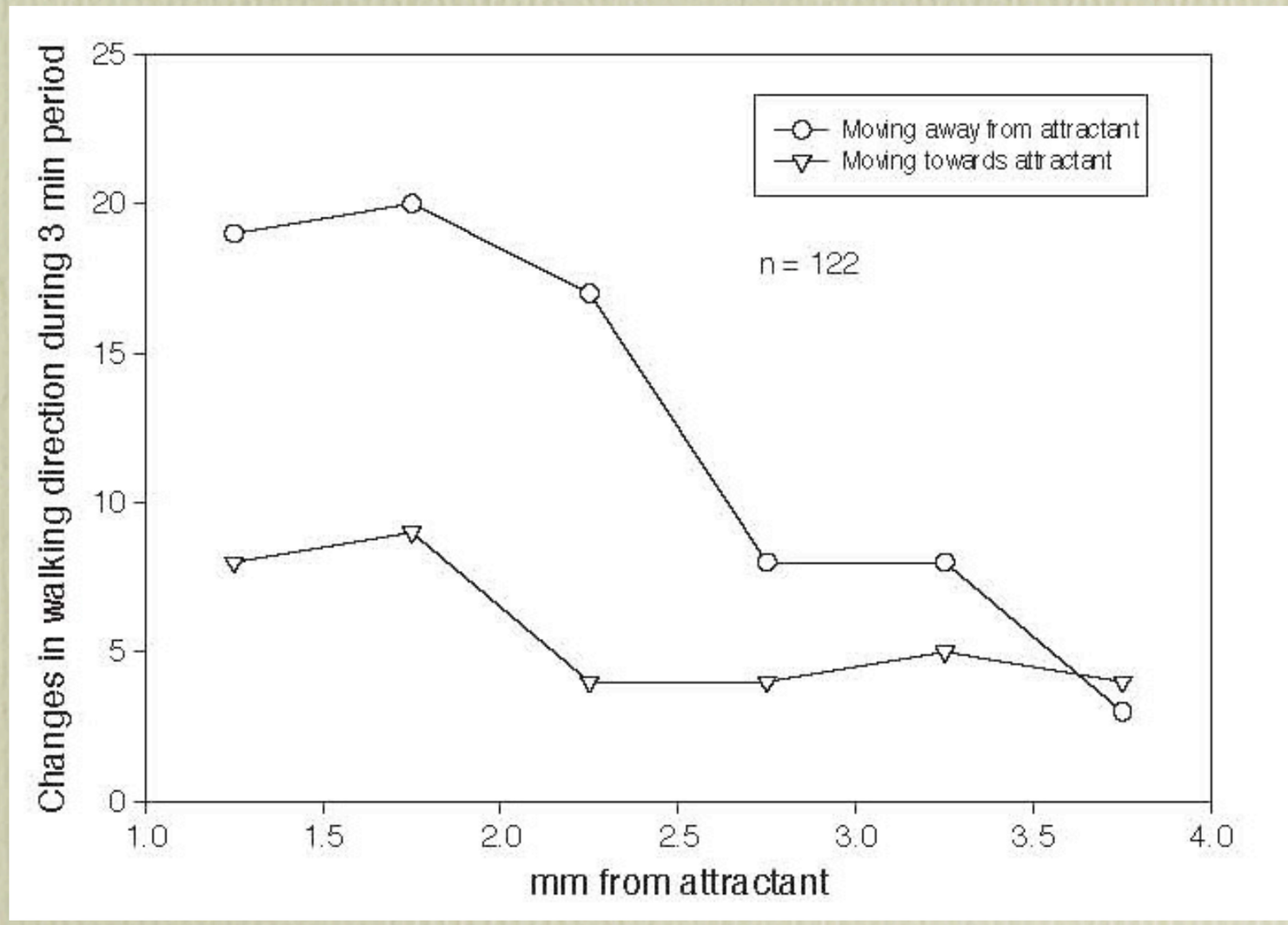
85% of time spent in patches



transient response to gradients

Transient response



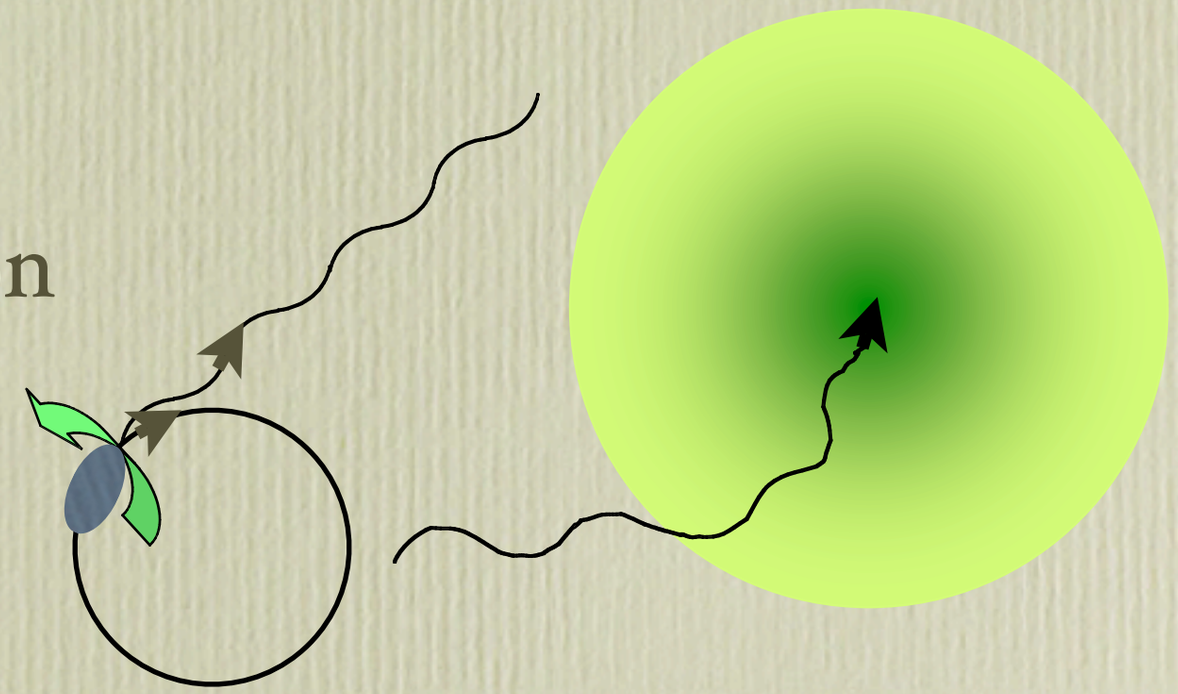


Fenchel 2004

Changes of direction

Helical klinotaxis

Helical motion



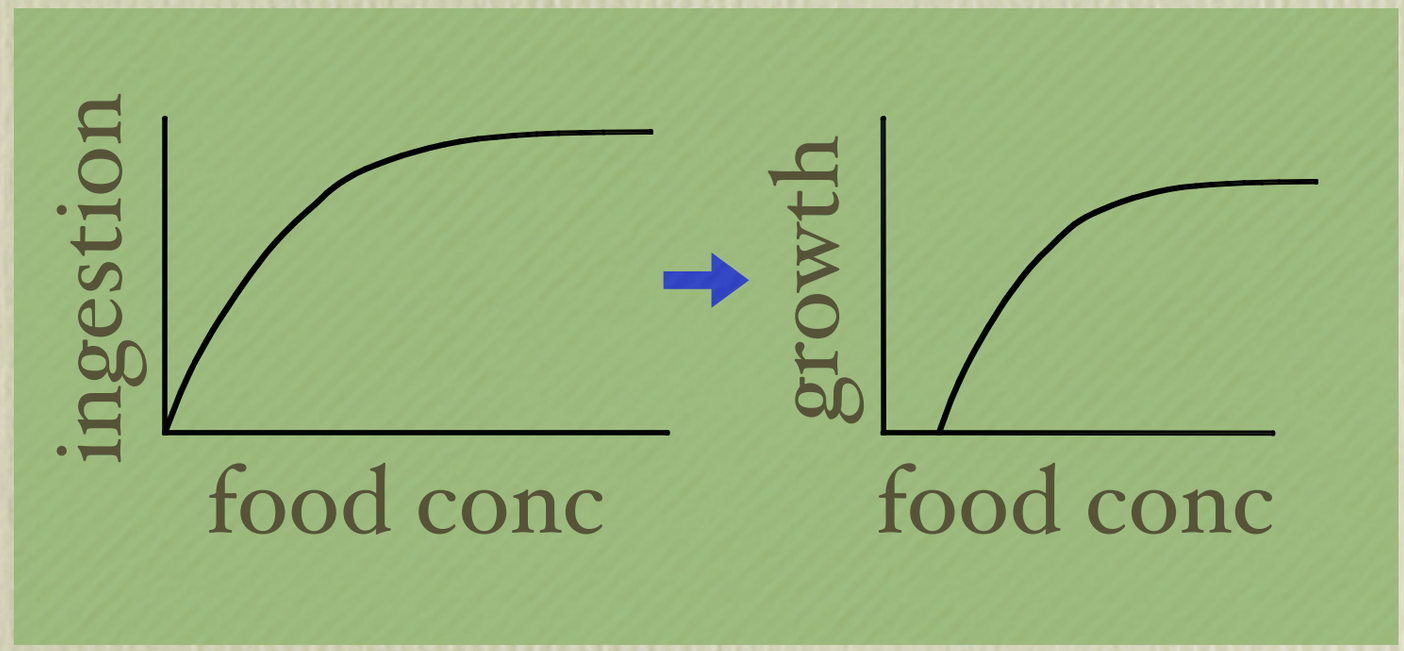
Rotation around the long axis (roll)
as a function of local concentration

What do we have so far?

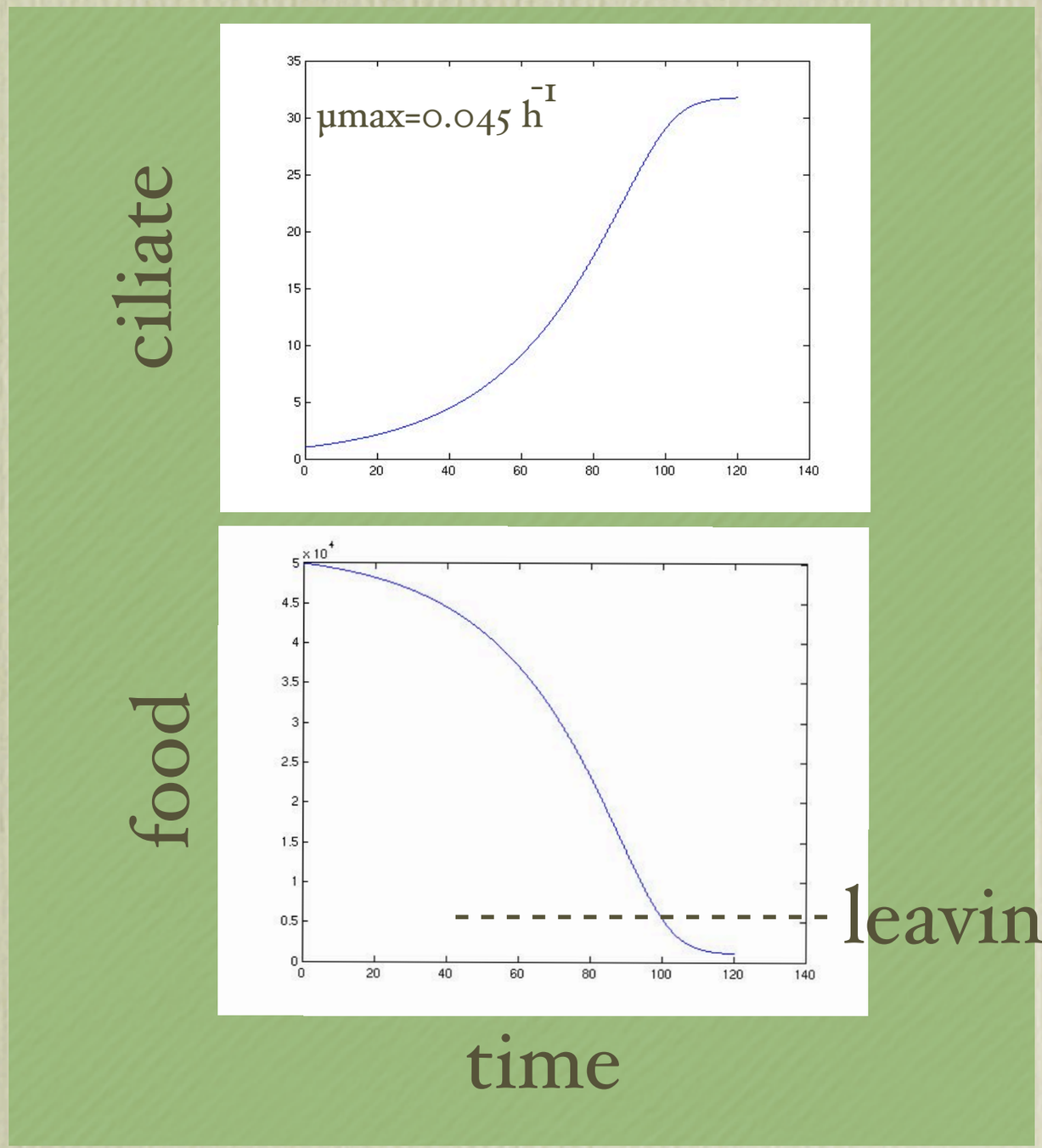
- Random encounter with patches, mainly diffusive process
- Response to both absolute concentrations and gradients
- Change in both speed and turning frequency

What happens when patch is exploited by successful ciliates?

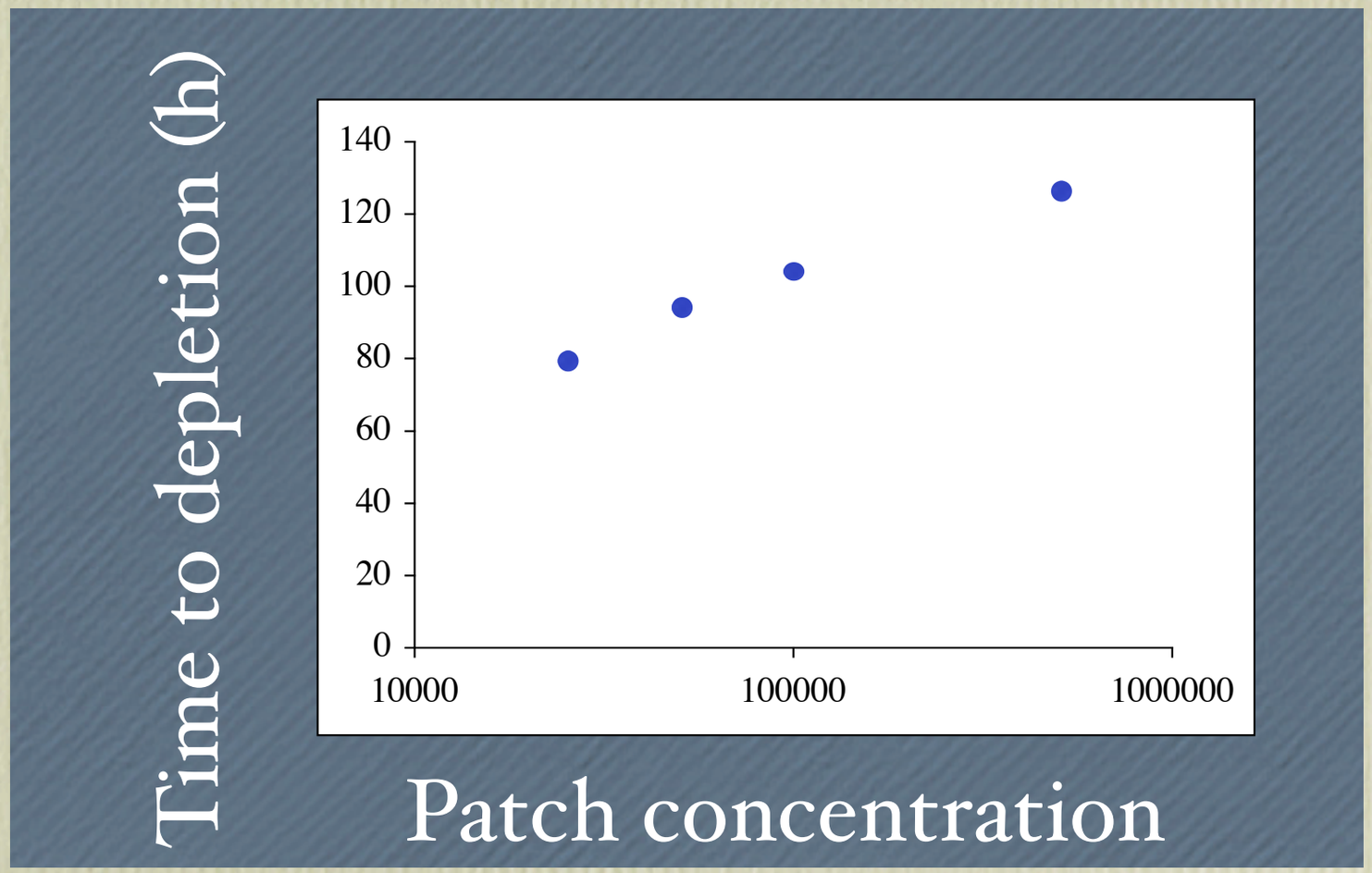
Food uptake and growth



Depletion of food patch

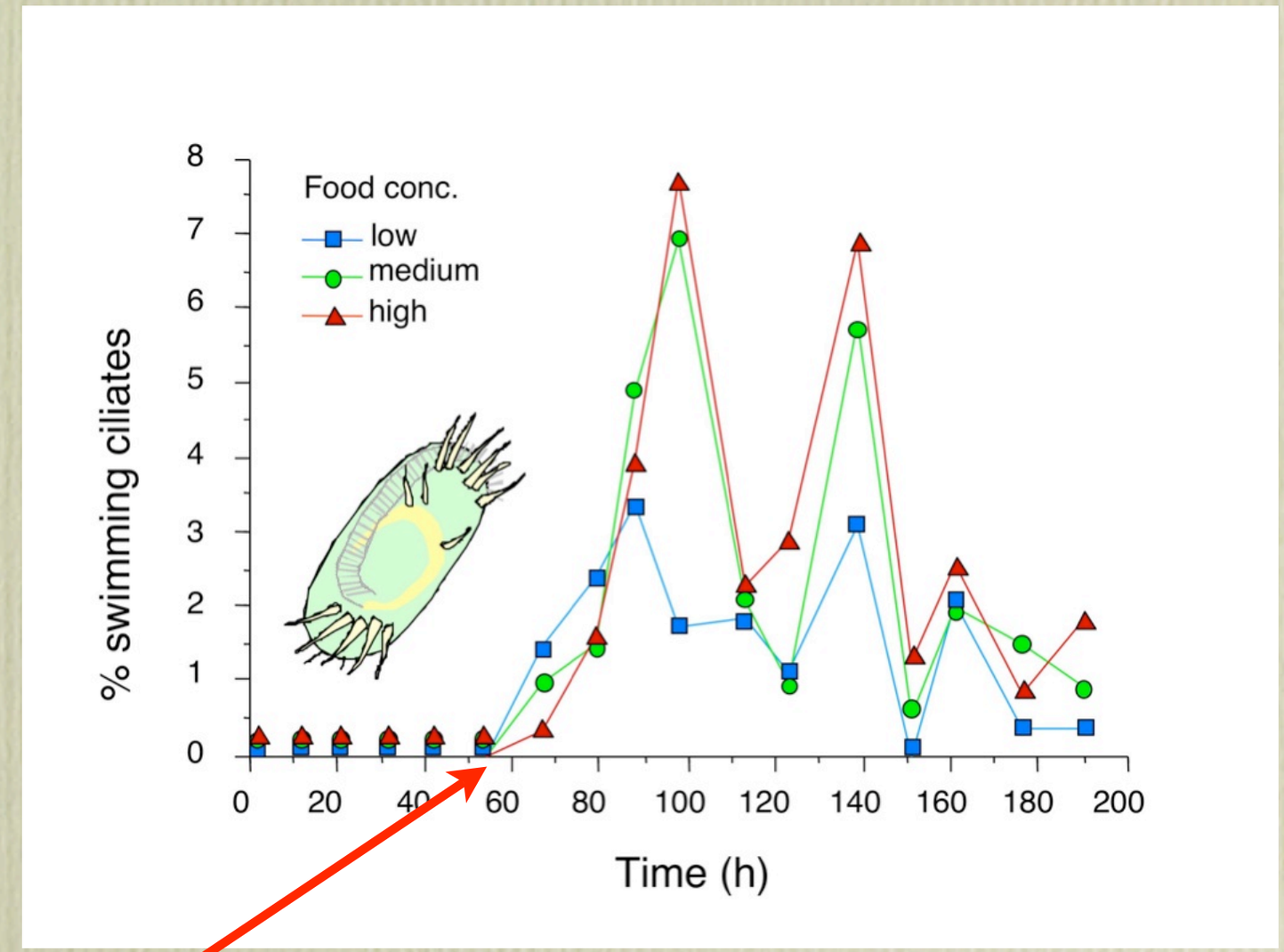


Time to deplete a patch



Expontial growth makes leaving time a non-issue

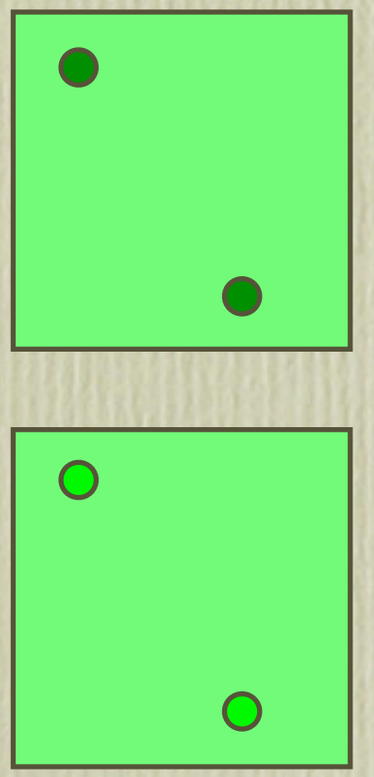
Dispersal behaviour when food is depleted



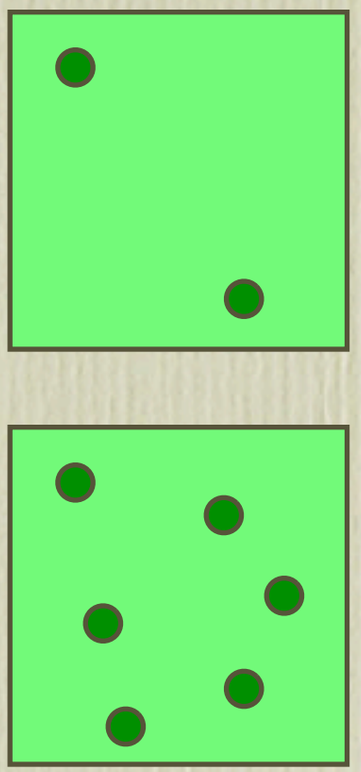
Patch depleted

Overall model of behavioural advantage

Patch intensity



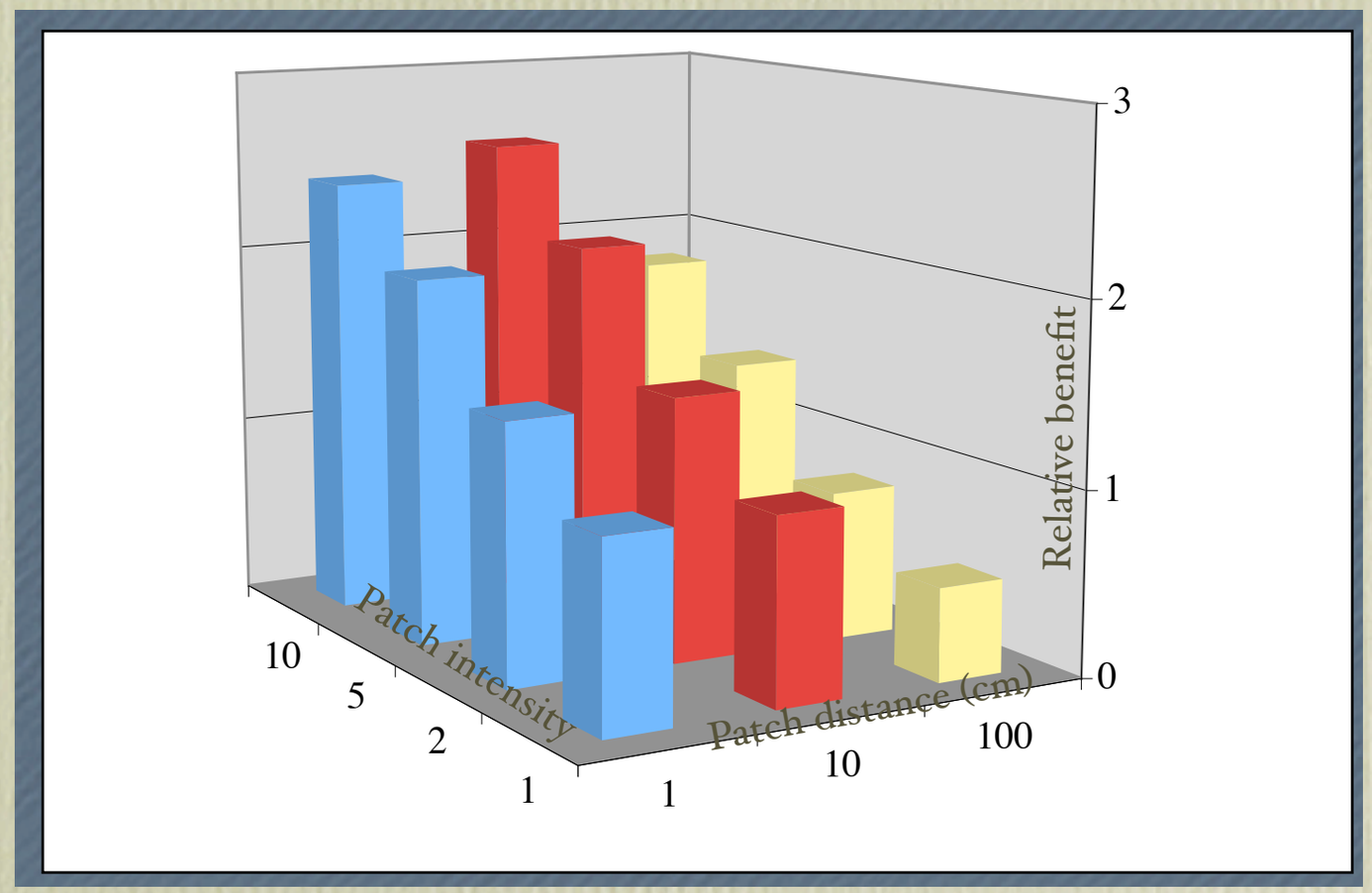
Patch density



Overall model of behavioural advantage

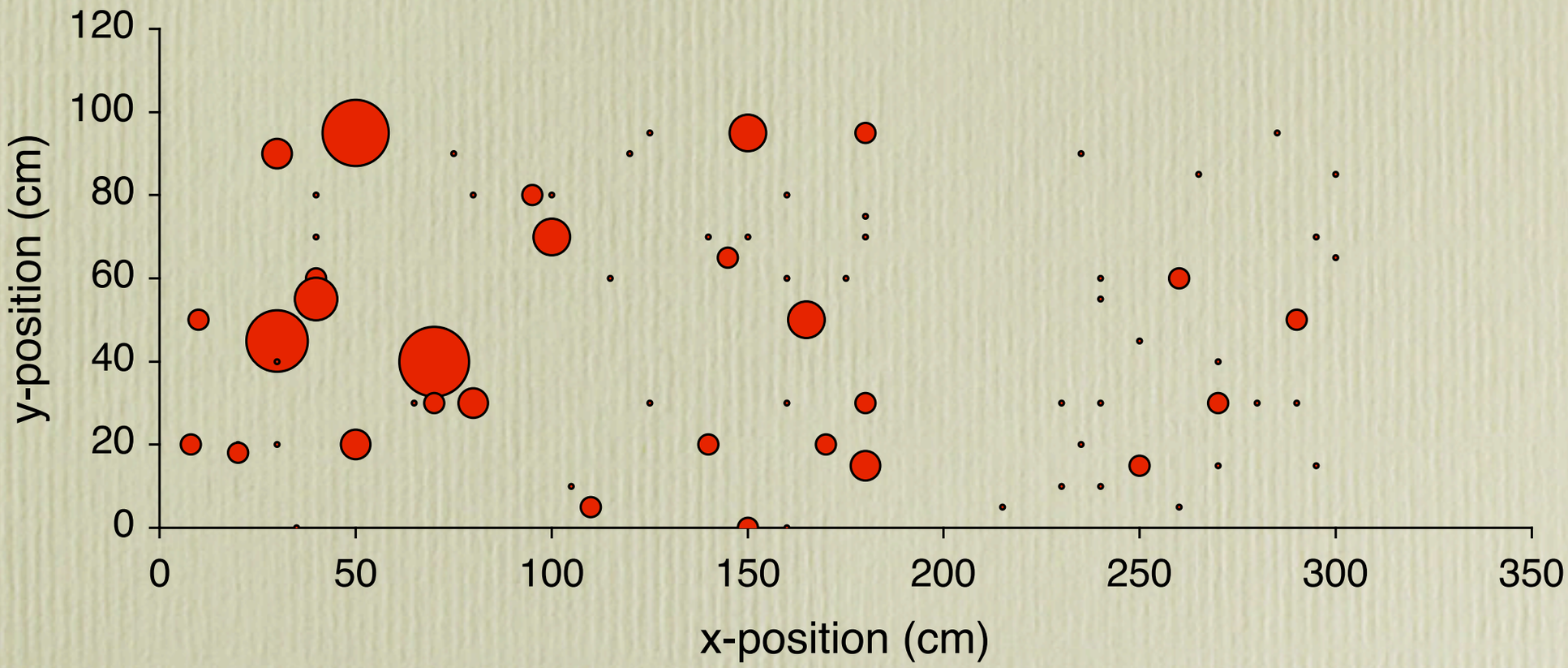
- A ciliate with behaviour disperses to a patch (travel time with no feeding)
- Exploitation leads to population growth and patch is depleted (depletion time)
- This is compared to a naive ciliate which moves randomly in the environment while feeding and growing

Overall advantage with patch behaviour



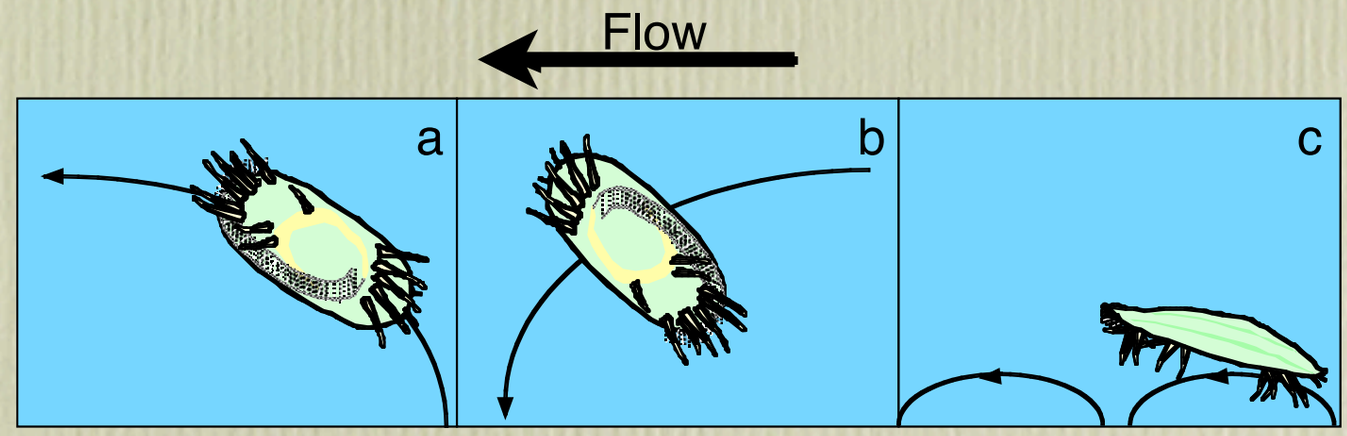
Microbial behaviour strongly increases turnover of carbon and nutrients!!

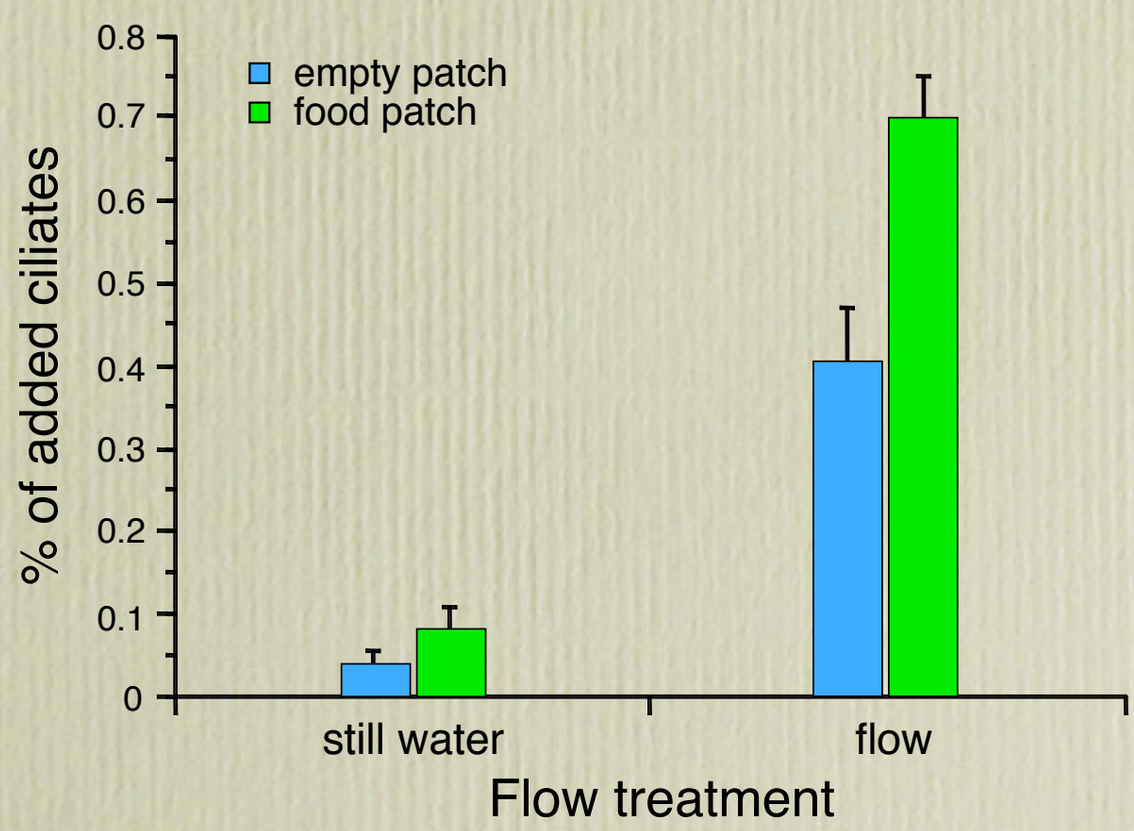
What is field patch distance?



Indications of 10-20 cm

In real life dispersal may be more intense





Conclusions

- "Microbes" often show behavioural responses that increase their fitness in a heterogenous world
- With biological-physical modelling it is possible to analyse behavioural mechanisms and predict ecological significance
- Microbial behaviour likely affects global biogeochemical fluxes

Thank you!