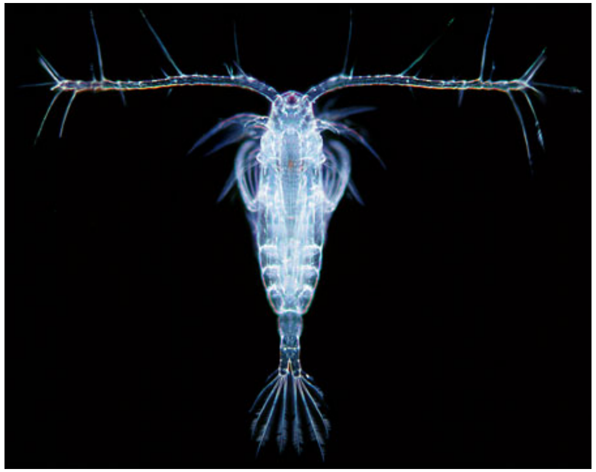
The Abdus Salam
International Centre for Theoretical Physics

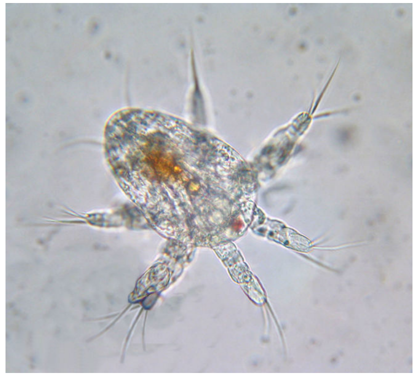
United Nations
Educational, Scientific and
Cultural Organization

IAEA
International Atomic Energy Agency

Advanced School on Complexity, Adaptation and Emergence in Marine Ecosystems

Mechanistic interactions in plankton, fitness and behaviour

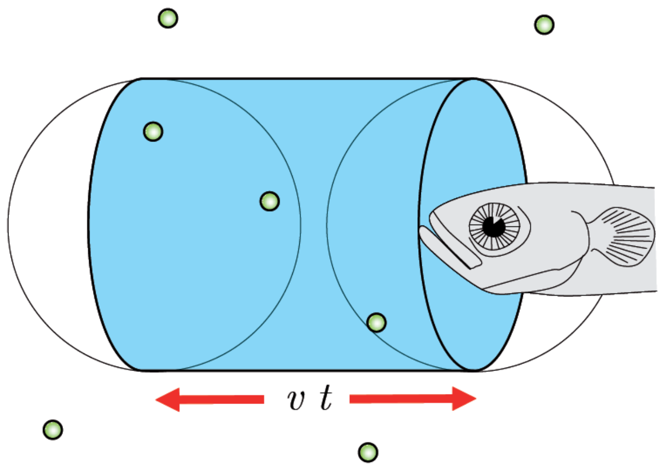


André W. Visser

DTU Aqua
National Institute of Aquatic Resources

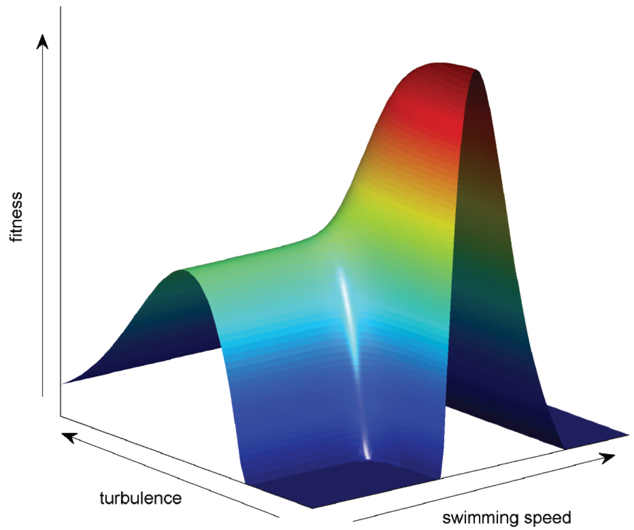
Mechanistic interactions in plankton, fitness and behaviour

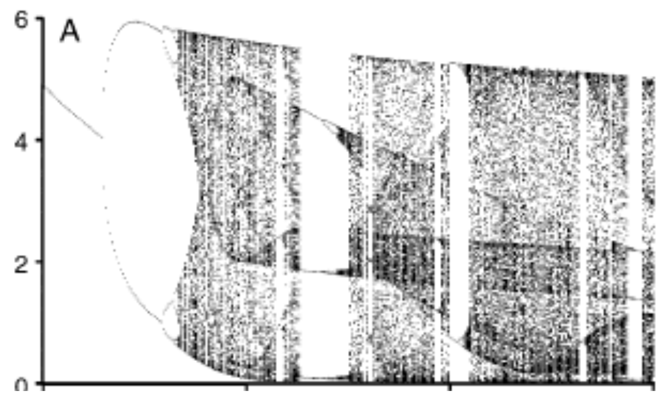


Mechanisms: encounter rate

Fitness and rational behaviour

Implications for populations





All organisms are confronted by 3 overarching tasks

Find food
Reproduce
Avoid predation

Those individuals that are most successful at this will have greater representation in future generations

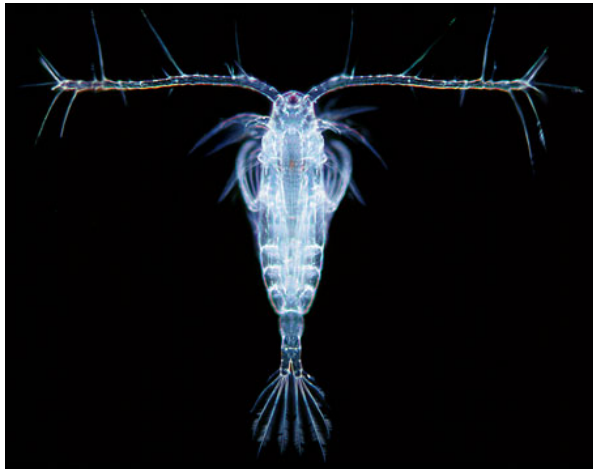
Behavioural traits that led to this success should therefore be expressed in the current population

Conditions are not static

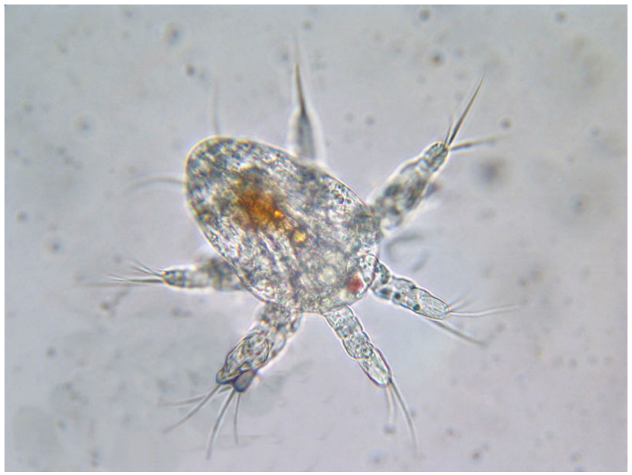
Adaptive traits are superior in an changing environment

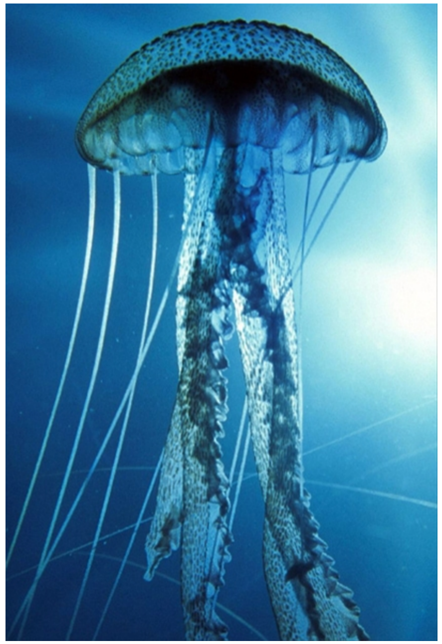
Natural selection acts at the individual level

Find food
Reproduce
Avoid predation



How are these factors determined by the **behaviour** of **individuals**





Individual interaction:

In the world of plankton

encounter rate is the currency of interaction

growth		**prey**
reproduction	**encounters with**	**mates**
mortality		**predators**

Encounter rates

concentration

Number of encounter partners (prey, mates, predator) per unit volume

detection distance

How far can an organism sense another.

Sensing ability and mode

- hydromechanical, chemical, visual, tactile

relative motion

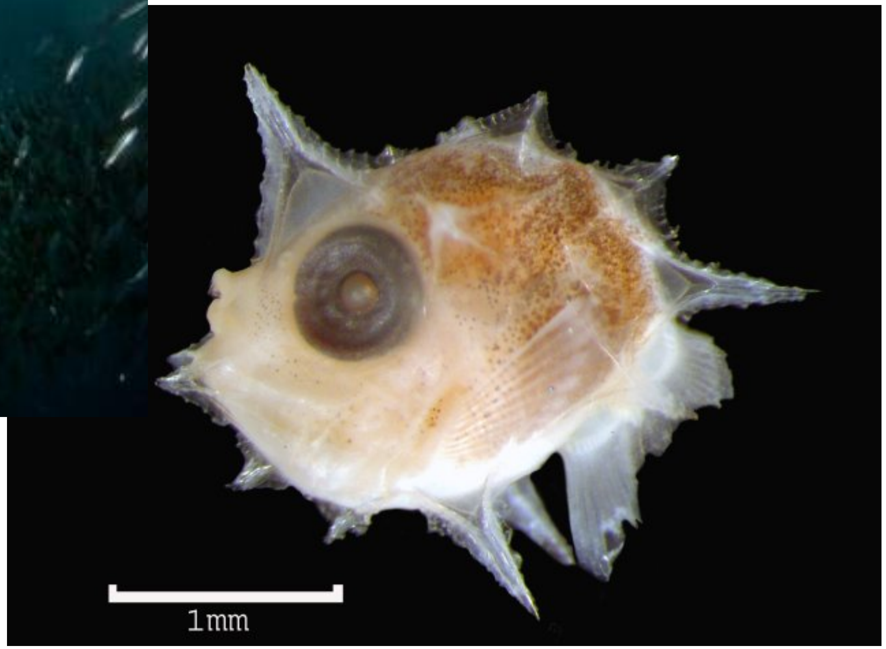
- Swimming
- Sinking
- Feeding current
- Turbulence

how they move

- Ballistic
- Diffusive

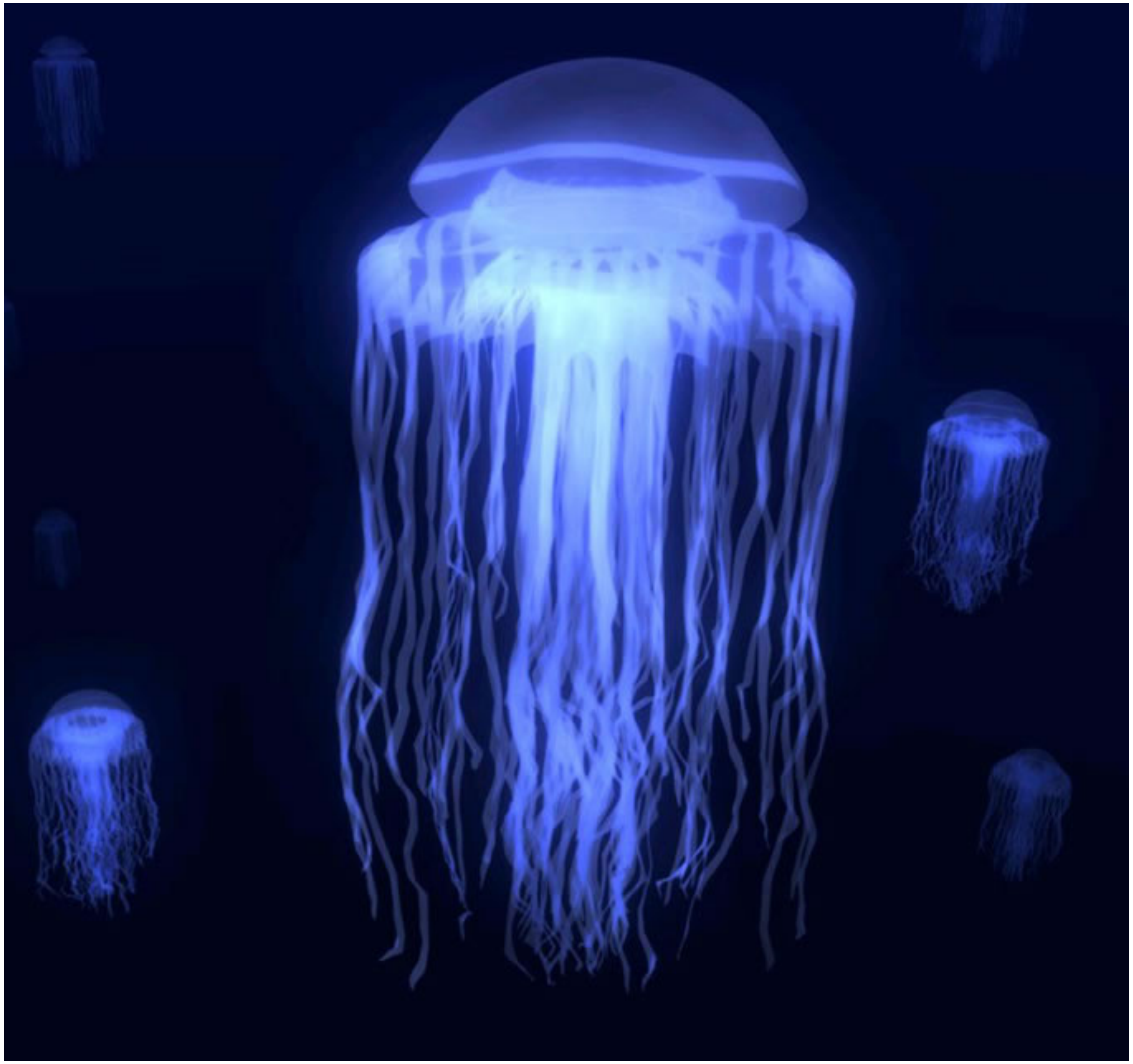
Visual

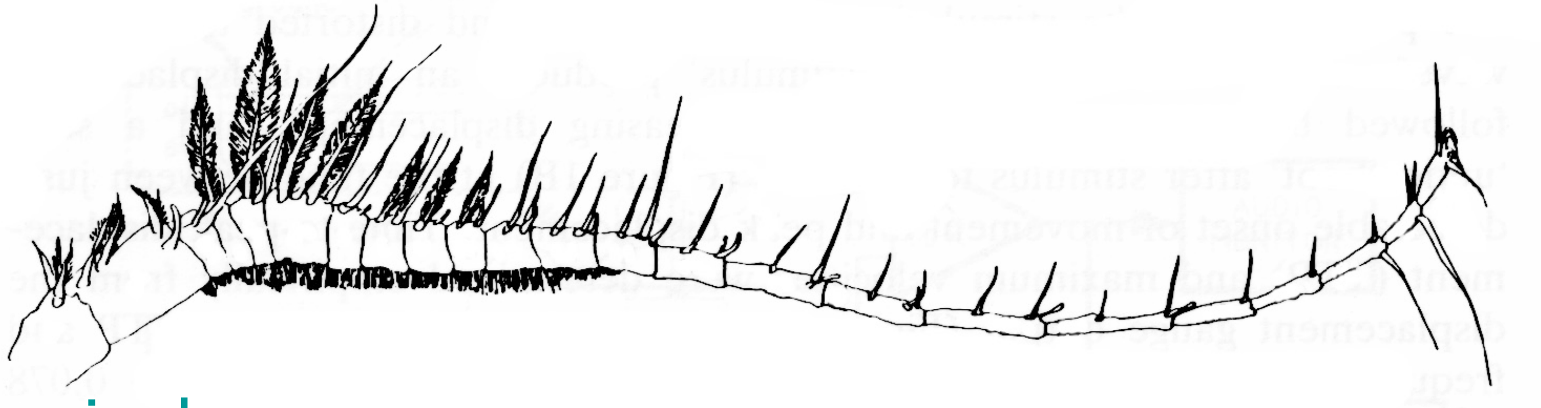
Limited by light penetration



Tactile

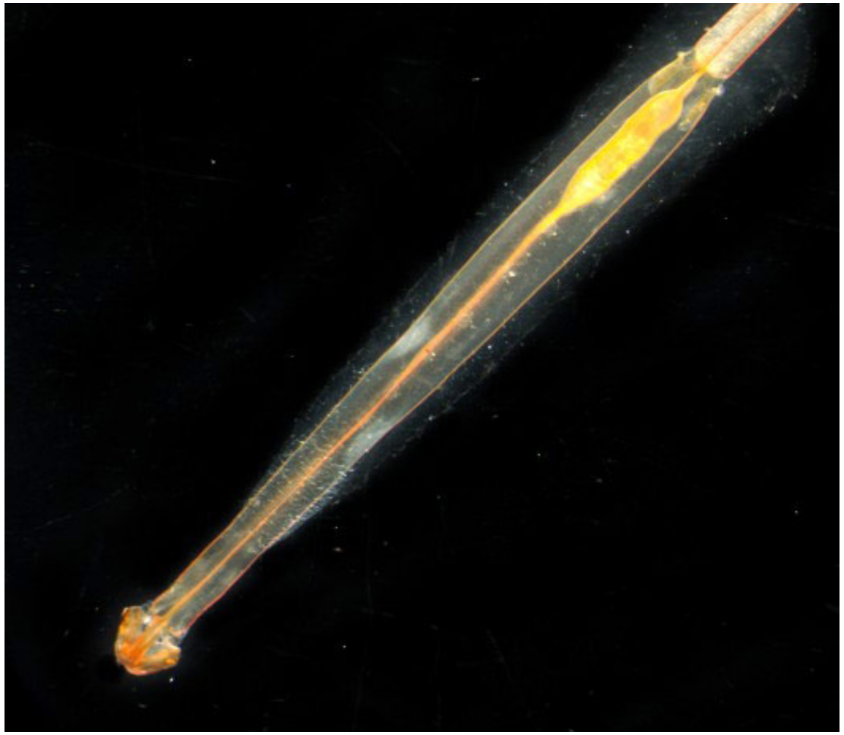
Requires prey to blunder into predator.

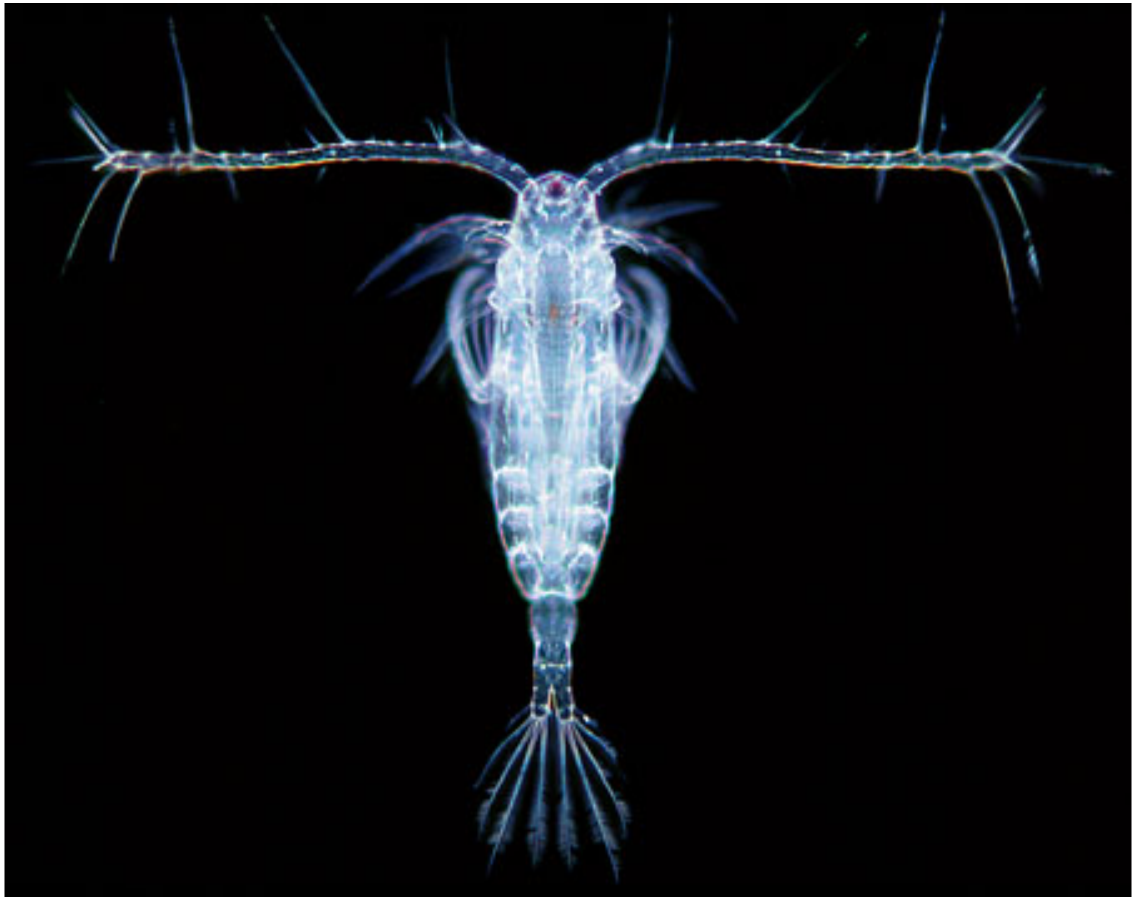




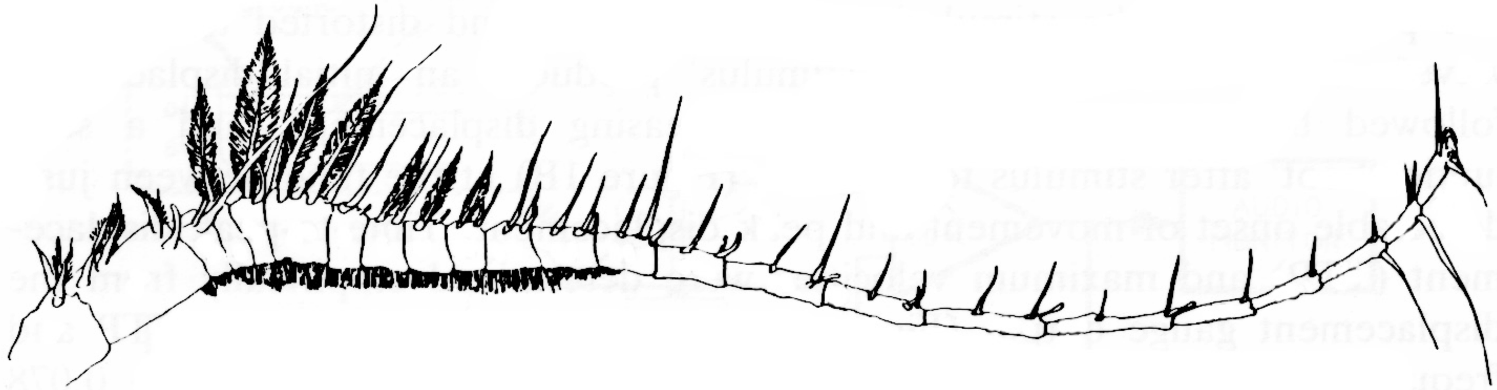
Hydromechanical

Small fluid disturbance cause setae to bend triggering neurological response.

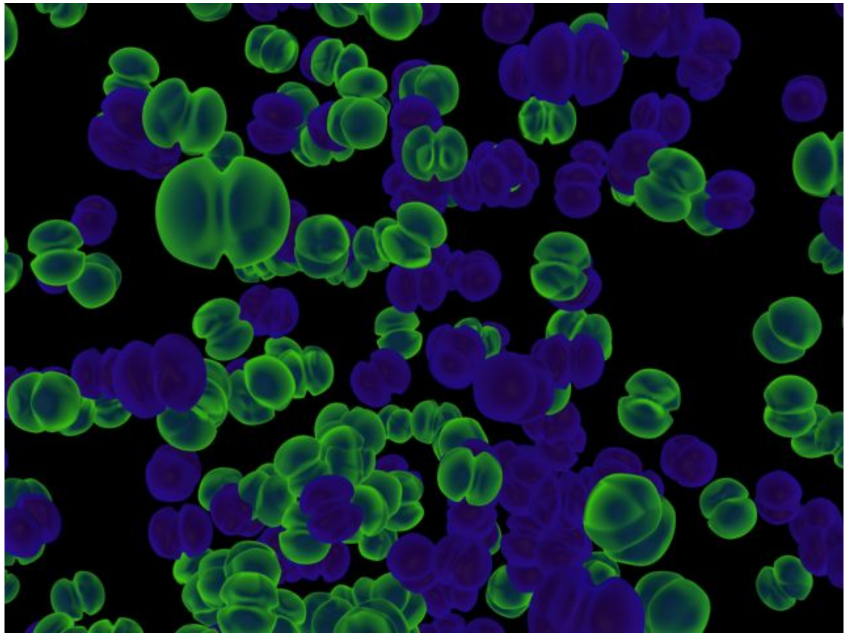




Chemical



Communication in Bacteria and protists
Locating mates; phermones,
Leaky prey
Depends on transport and dispersion of chemical materials

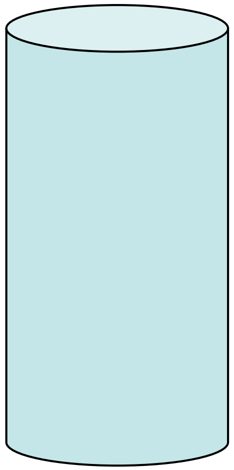


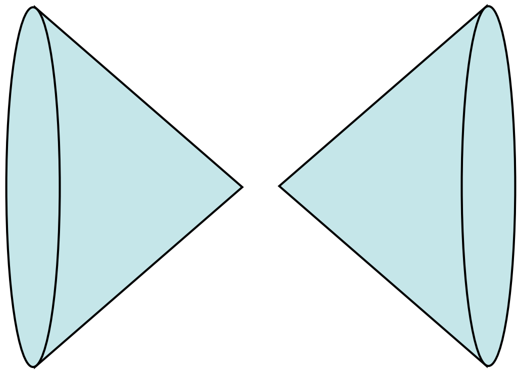
Sound

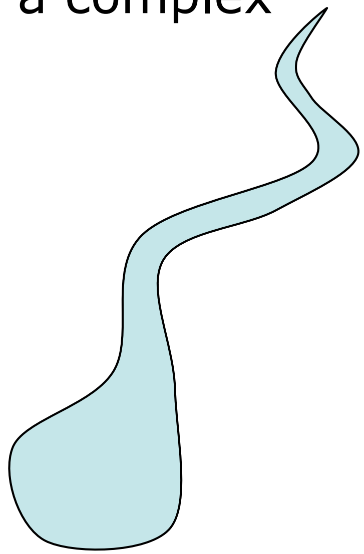
Sound travels a long way in the oceans (sonar)

Important for marine mammals and fish but not for zooplankton

How marine organisms sense each other is in general a complex geometric problem



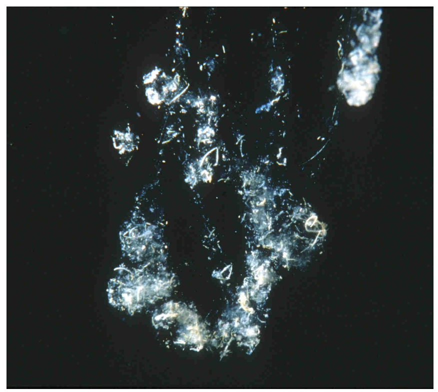




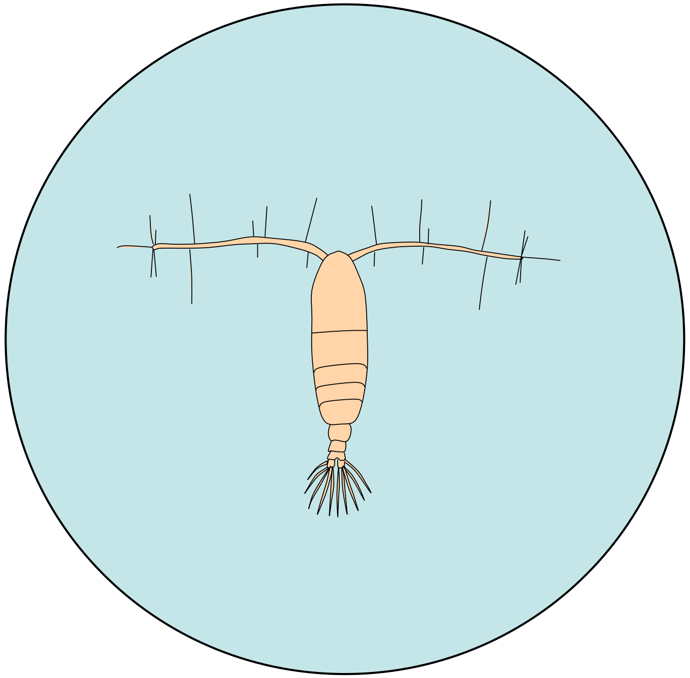
jellyfish

fish

chemical trail



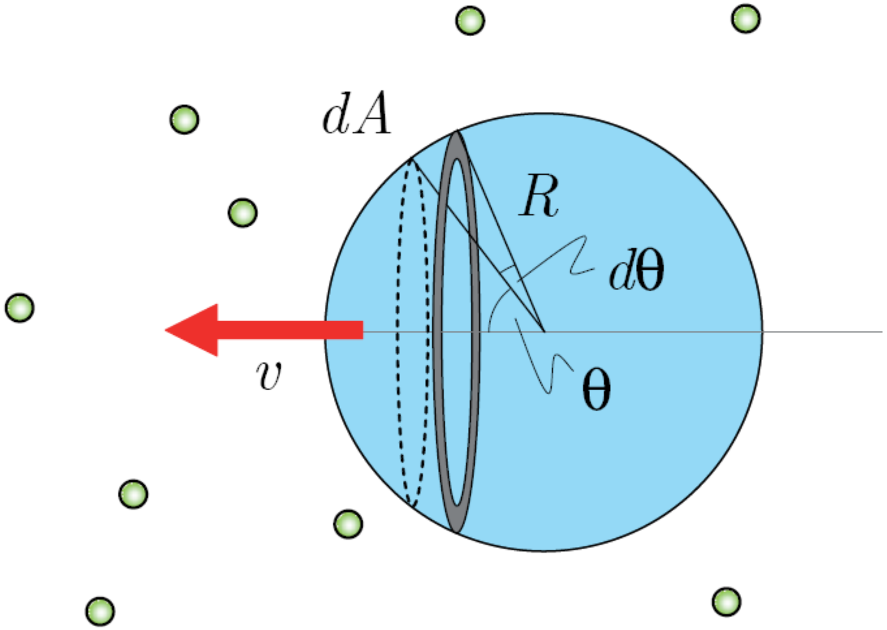
How marine organisms sense each other is in general a complex geometric problem



Simplest is a spatially uniform detection distance R:
This traces out a spherical detection zone in 3D

Encounter rates

Simplest and most robust model
is a translating sphere.



How many particles enter the sphere
per unit time ?

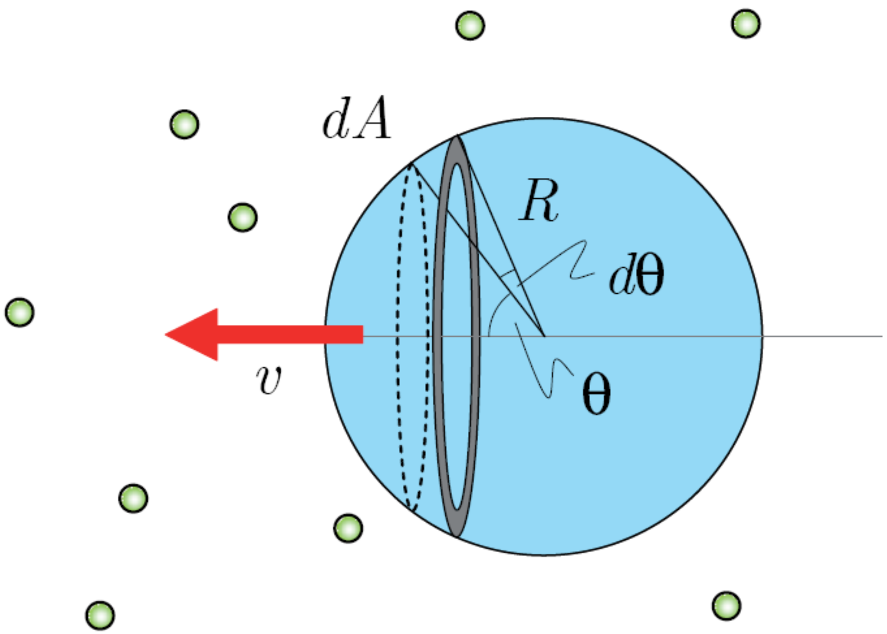
Partial encounter rate through a
small annular ring *dA*

$$dZ = Cv\cos\theta \; dA$$

$$= Cv2\pi R^2 \sin\theta\cos\theta \, d\theta$$

Integrating
$$Z = \int_0^{\pi/2} Cv2\pi R^2 \sin\theta\cos\theta \, d\theta = \pi R^2 Cv$$

Encounter rates



That is:

$$Z = pR^2Cv$$

Encounter rate

Detection distance

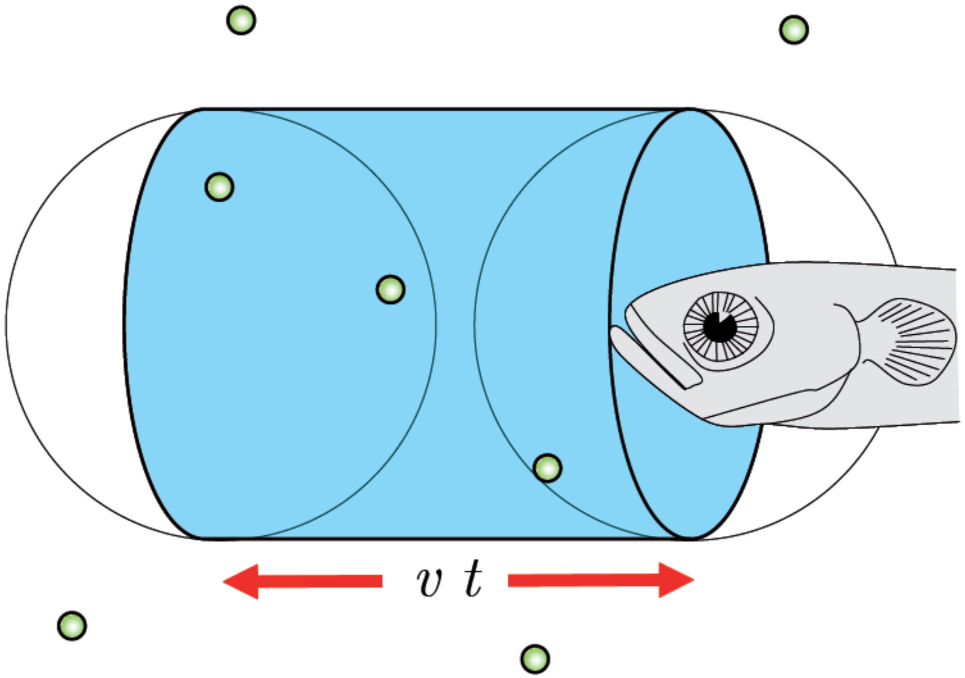
Prey concentration

Swimming speed

Encounter rates

$$Z = pR^2Cv$$

is the rate at which one “predator” encounters prey



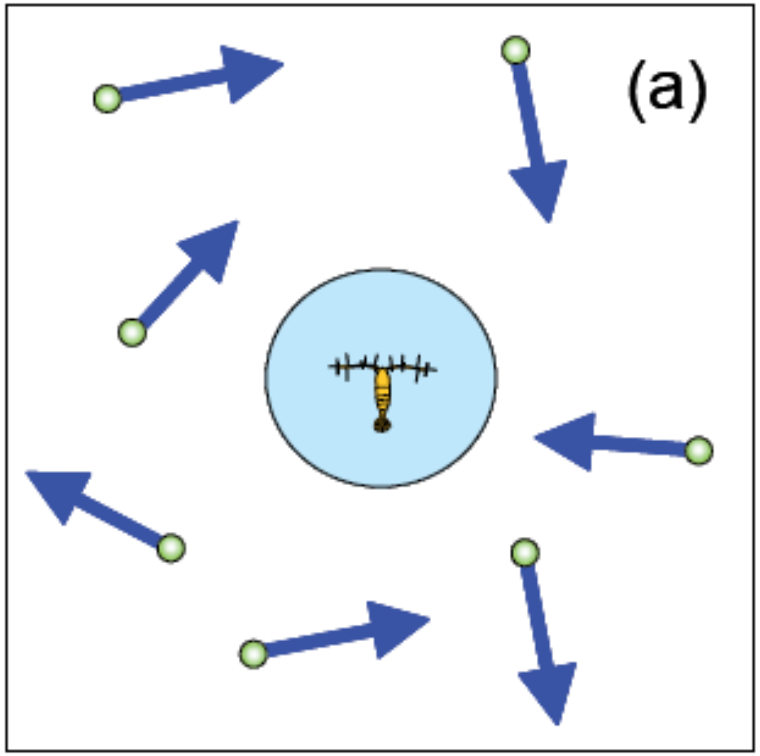
= the rate at which a tube of radíus R is swept out multiplied by the concentration

If there are P “predators” per unit volume then the rate of encounter events is

$$E = pR^2PCv$$

Encounter rates

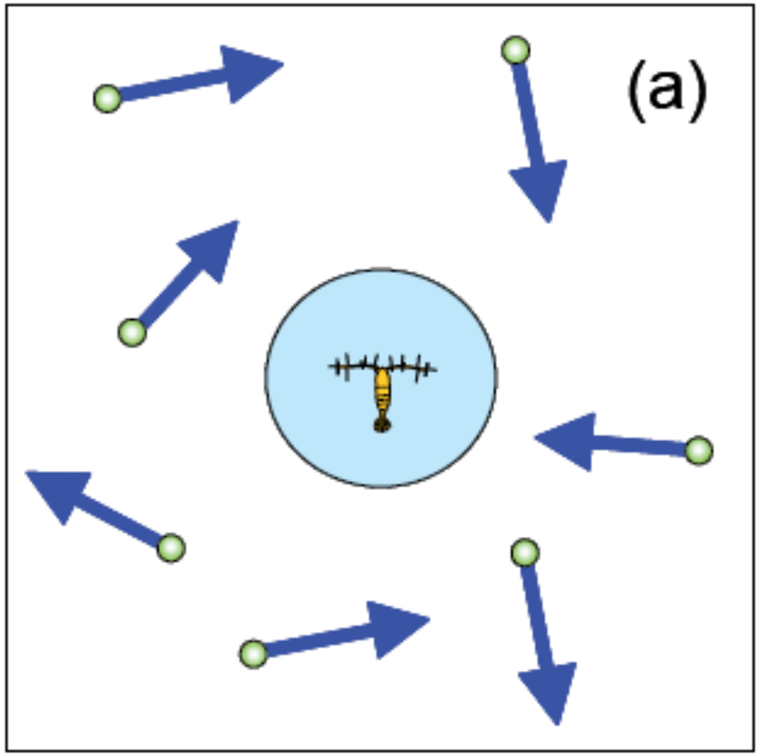
moving prey and stationary ambush predator



Encounter rates

moving prey and stationary ambush predator

It takes 2 to tango: encounters rates can be viewed either from the point of view of the **detector** or **detectee**



Count events:

$$E = PCb$$

where β is the encounter kernel which has units volume/time

$$Z_P = E / P = Cb$$

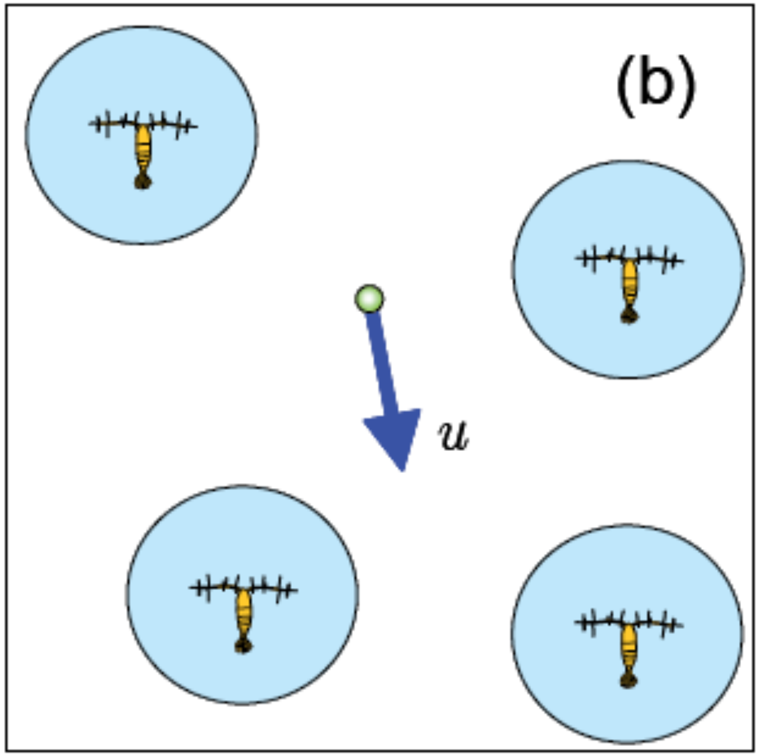
$$Z_C = E / C = Pb$$

Encounter rates

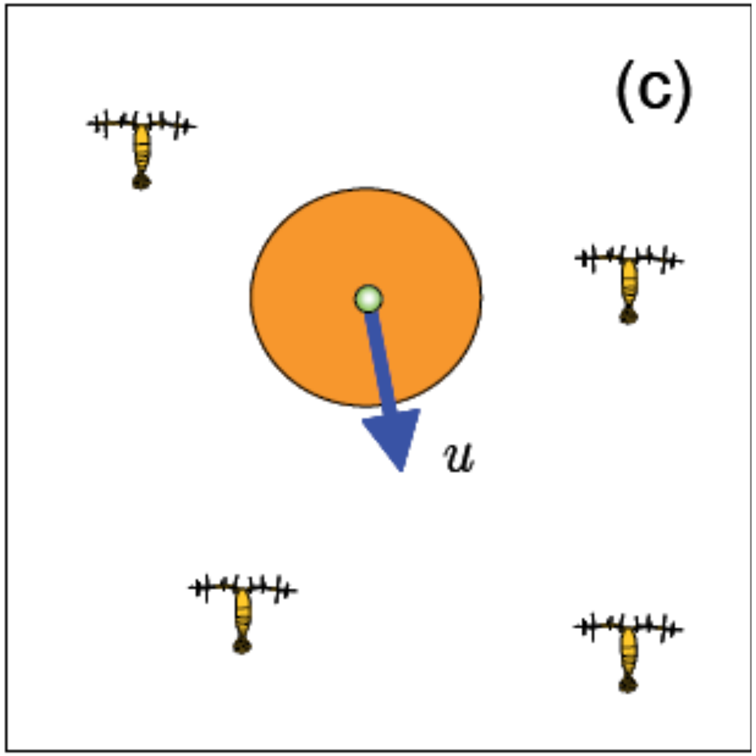
$$Z_P = E/P = Cb$$

$$Z_C = E/C = Pb$$

Change emphasis to a single moving “prey”



Equivalent to a moving “prey” with a spherical danger zone radius R

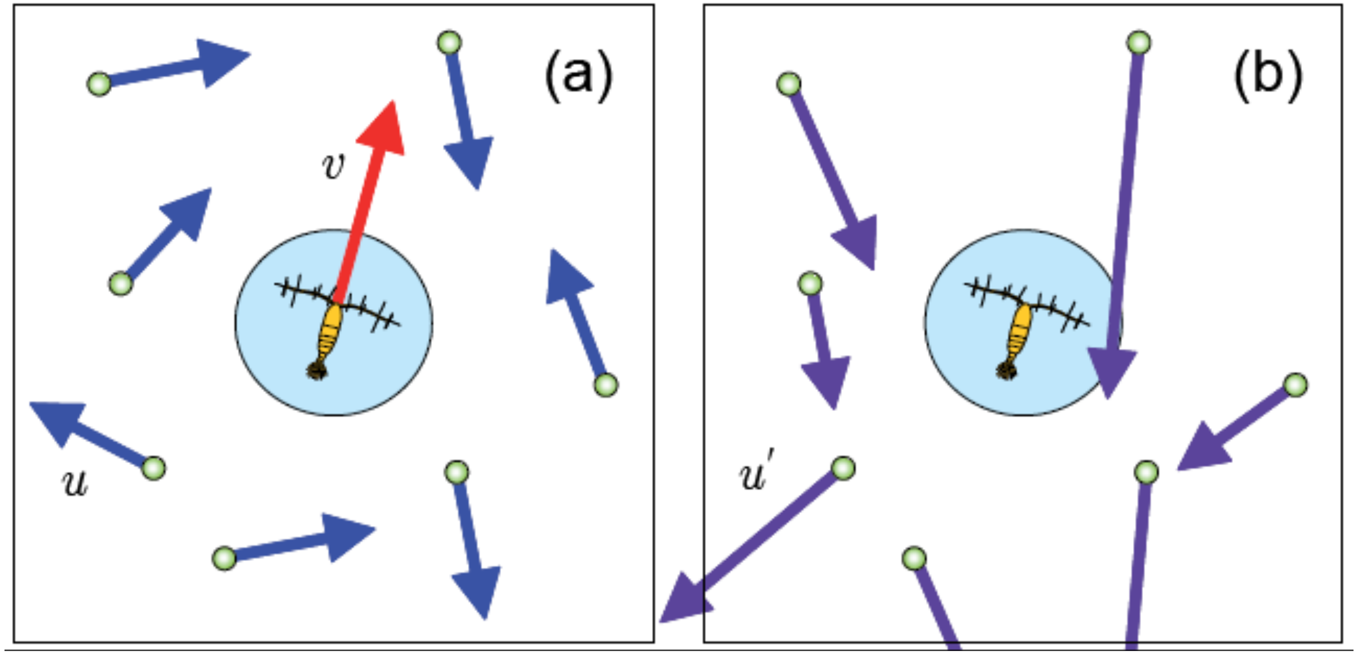


Same form as for a moving “predator” so it immediately follows

$$Z_P = pR^2Cu$$

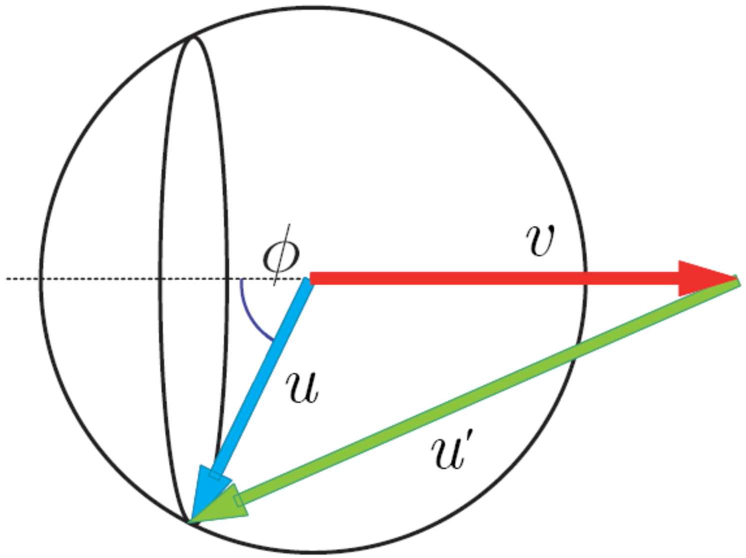
Encounter rates

When both predator and prey are moving



Encounter rates

When both predator and prey are moving at a constant speed



Relative speed at angle ϕ

$$u' = \sqrt{v^2 + u^2 + 2uv\cos(\pi - \phi)}$$

Integrating over all possible angles

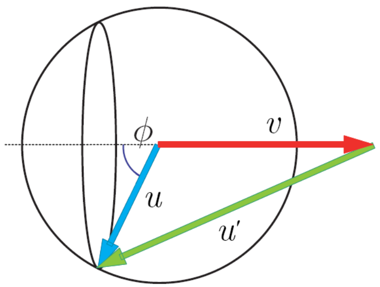
$$\langle u' \rangle = \frac{1}{4\pi}\int_0^{\pi} \sqrt{v^2 + u^2 + 2uv\cos(\pi - \phi)}\, 2\pi \sin\phi \, d\phi$$

$$Z = \pi R^2 C \langle u' \rangle = \pi R^2 C \frac{|u+v|^3 - |u-v|^3}{6uv}$$

Gerritsen & Strickler 1977

Encounter rates

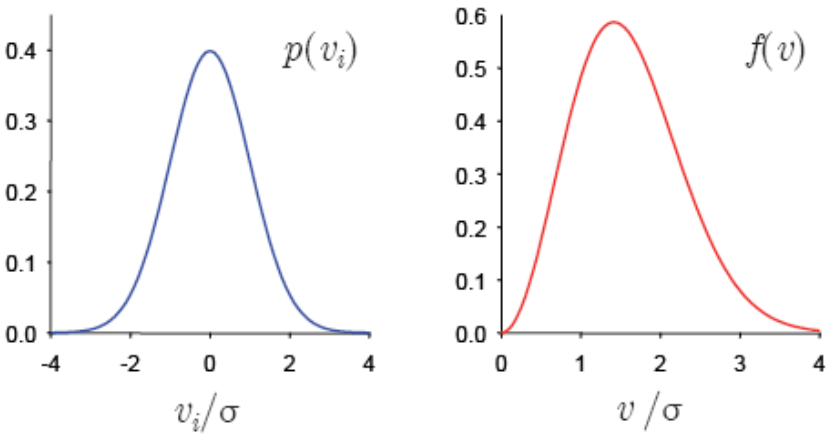
When both predator and prey are moving with different speeds



A simpler and more complete expression

Swimming speeds have a Raleigh distribution

(1)



Probability distribution of
(1) a velocity component and
(2) speed

Kinetic Theory

(2)

$$Z = pR^2C\sqrt{u^2 + v^2}$$

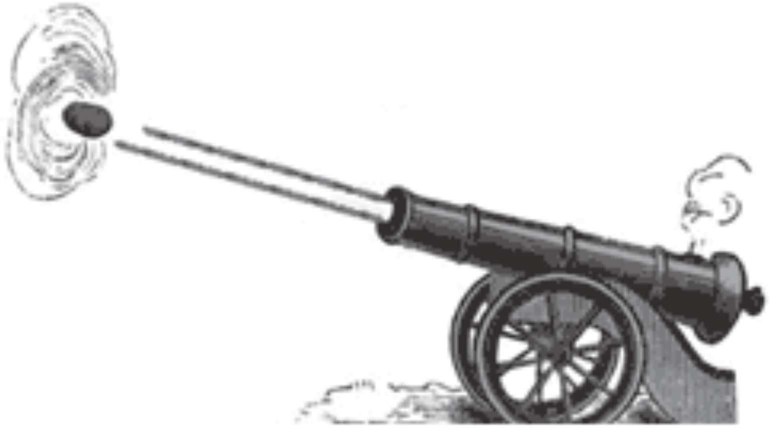
Predator speed

Prey speed

Evans 1989

Ballistic motion

What we have considered so far is termed ballistic motion



That is, organisms, both predator and prey move in straight lines

Not always realistic

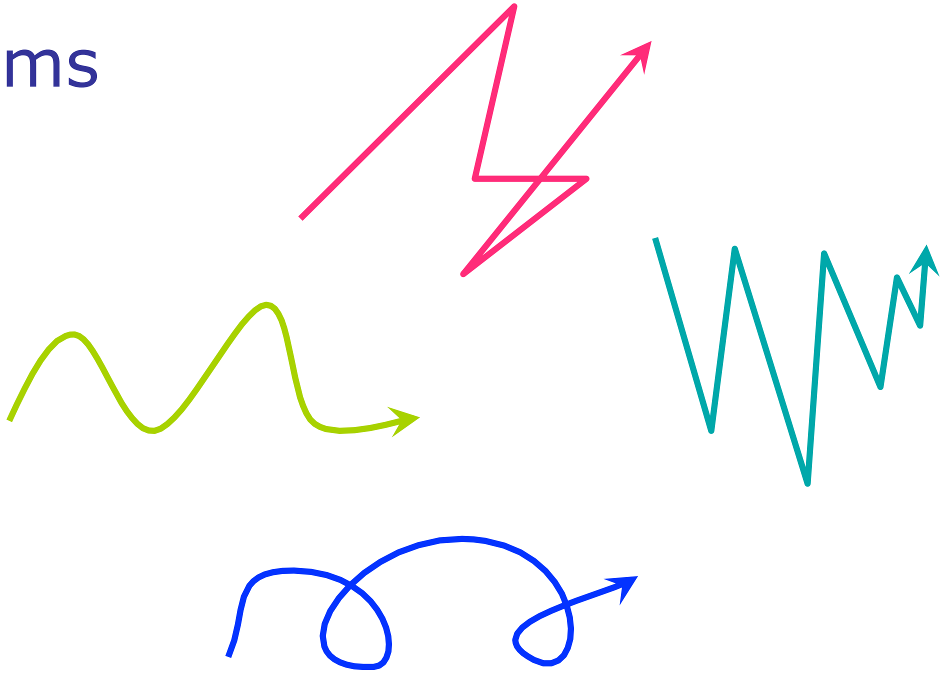
Motility of organisms

Erratic

Sinuous

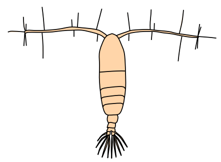
Helical

Hop - sink

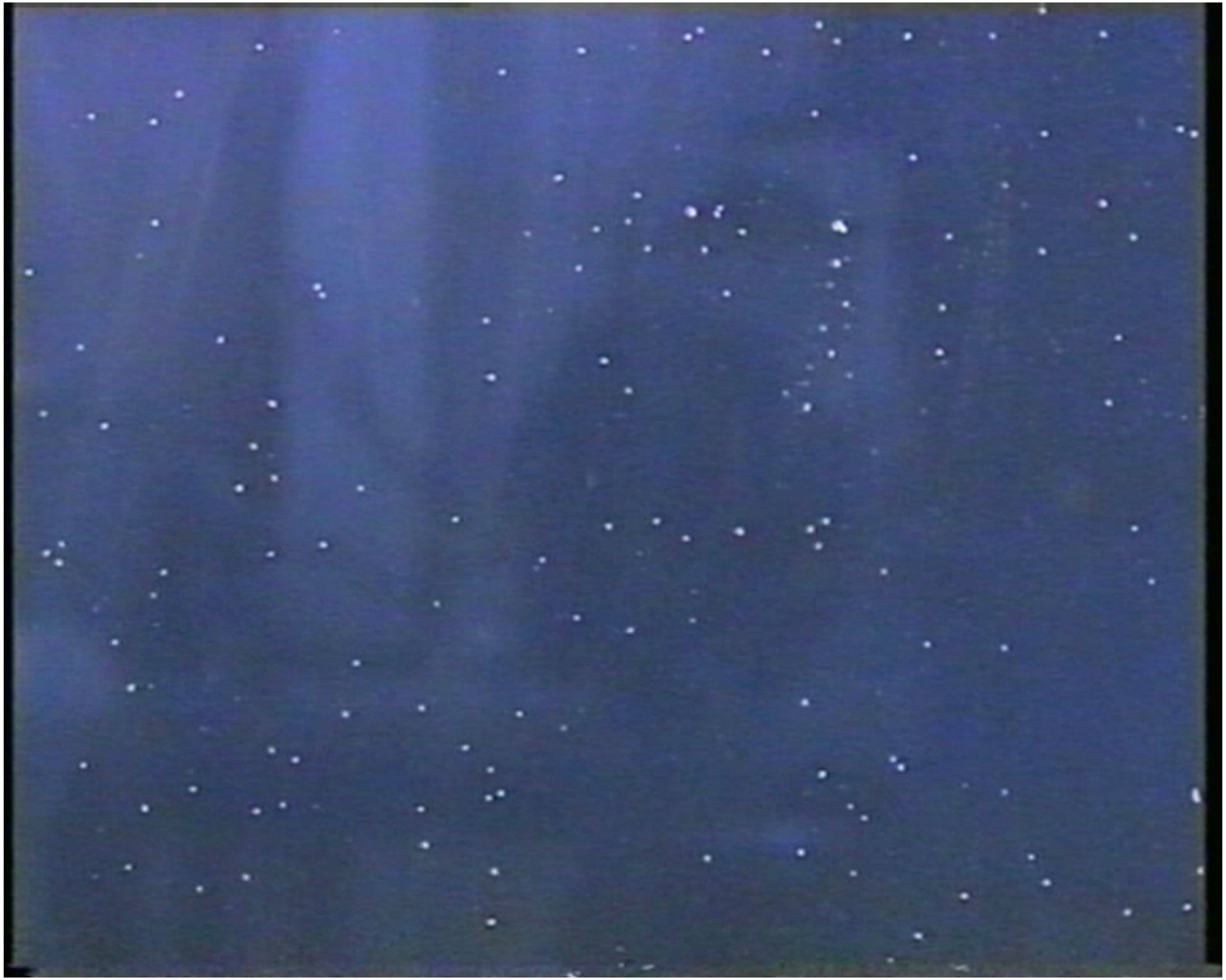


some element of randomness

Random walk motility



Diffusive motion – and has implications for
Encounter rates



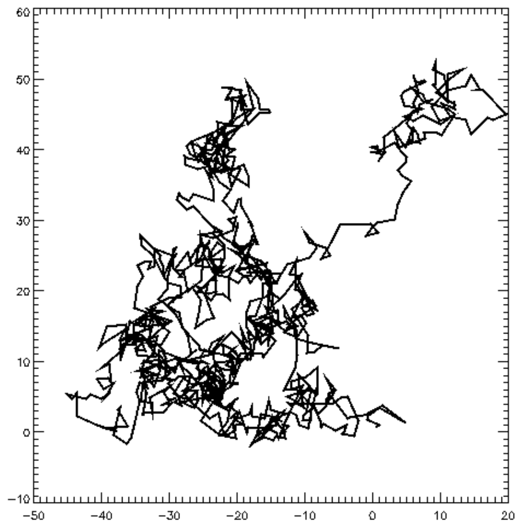
Random walks

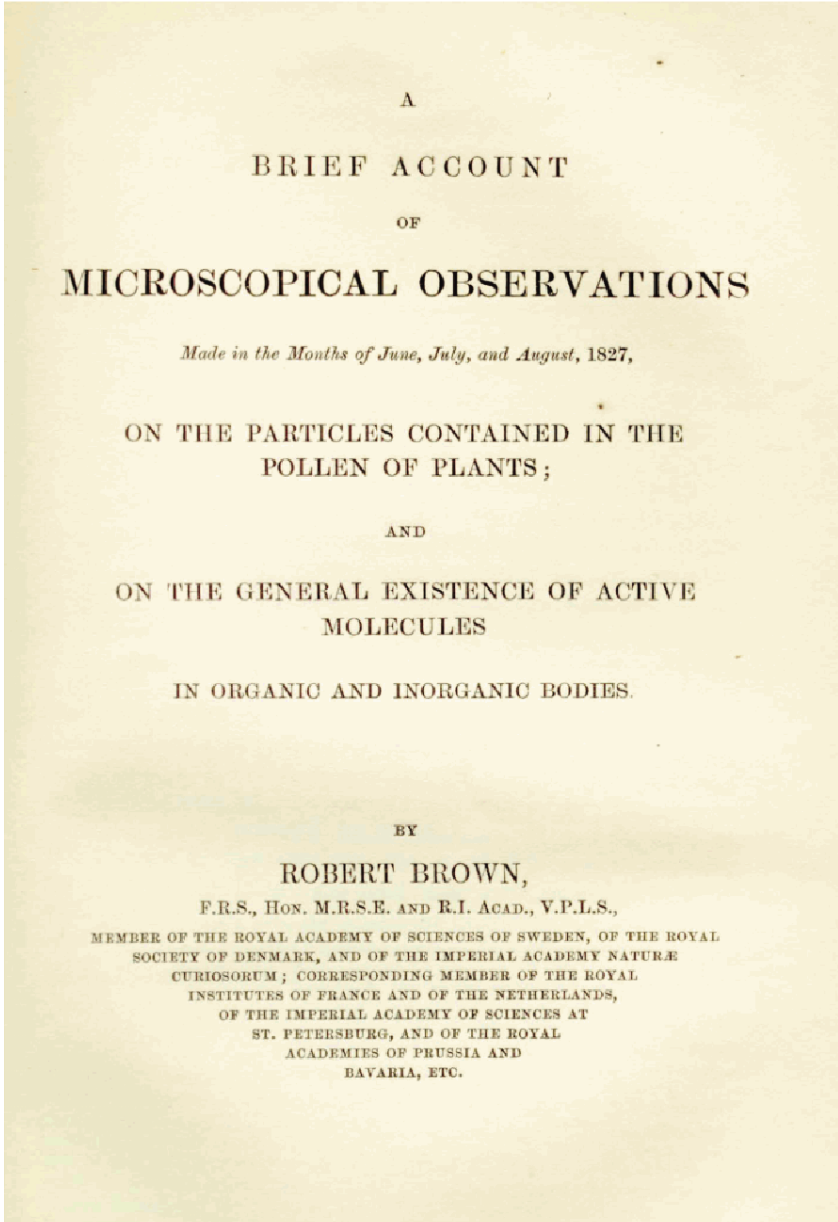
Brownian motion

A mechanistic description of diffusion

Random motility of organisms
and what this means for encounter rates

Brownian motion





A

BRIEF ACCOUNT

OF

MICROSCOPICAL OBSERVATIONS

Made in the Months of June, July, and August, 1827,

ON THE PARTICLES CONTAINED IN THE POLLEN OF PLANTS;

AND

ON THE GENERAL EXISTENCE OF ACTIVE MOLECULES

IN ORGANIC AND INORGANIC BODIES.

BY

ROBERT BROWN,

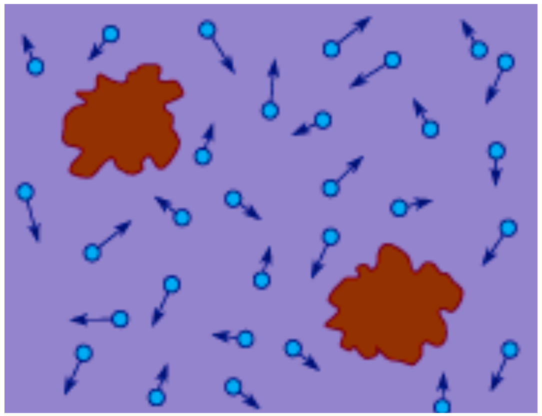
F.R.S., HON. M.R.S.E. AND R.I. ACAD., V.P.L.S.,

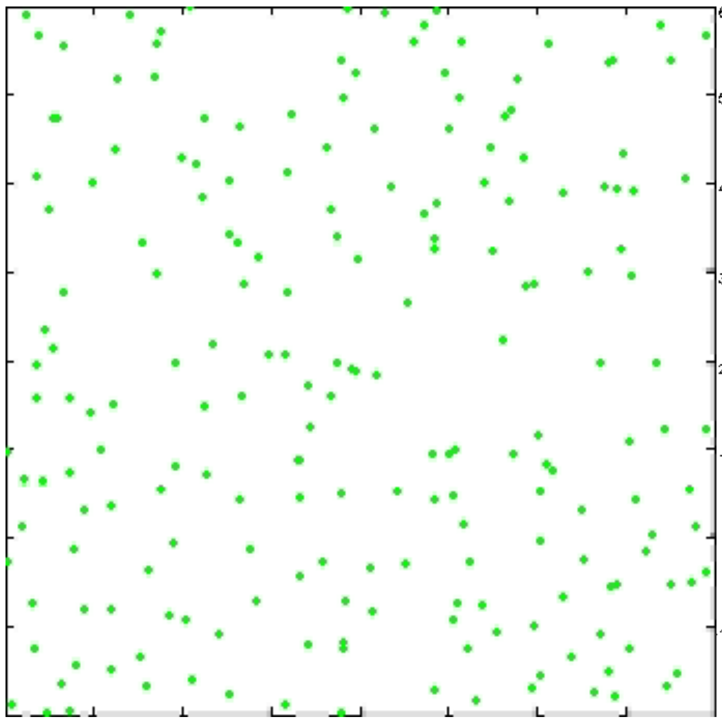
MEMBER OF THE ROYAL ACADEMY OF SCIENCES OF SWEDEN, OF THE ROYAL SOCIETY OF DENMARK, AND OF THE IMPERIAL ACADEMY NATURÆ CURIOSORUM; CORRESPONDING MEMBER OF THE ROYAL INSTITUTES OF FRANCE AND OF THE NETHERLANDS, OF THE IMPERIAL ACADEMY OF SCIENCES AT ST. PETERSBURG, AND OF THE ROYAL ACADEMIES OF PRUSSIA AND BAVARIA, ETC.

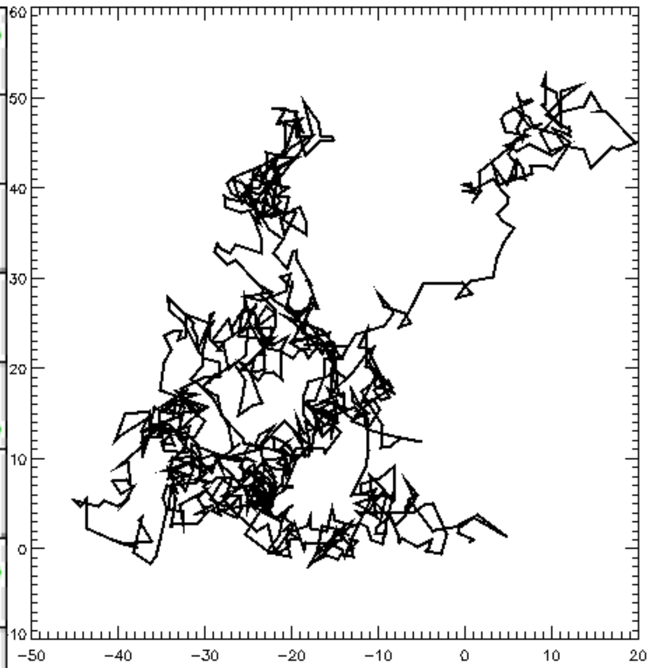
Brownian motion & Diffusion

1905

"On the motion of small particles suspended in liquids at rest required by the molecular-kinetic theory of heat." (Brownian motion paper) (May 1905; received 11 May 1905) *Annalen der Physik*, 17(1905), pp. 549-560.







Brownian motion & diffusion

Brownian motion due to randomly directed impulses from collisions with thermally excited molecules

$$D = \frac{KT}{6\pi\mu a}$$

K = Boltzmann's constant 1.38×10^{-16} g cm^2 s^{-2} $^oK^{-1}$

T = temperature in ^oK

μ = viscosity

bacteria
colloids

$a \approx 1\ \mu$

$D \approx 10^{-6}$ to 10^{-7} cm^2/s

Einstein's physical explanation of Brownian motion has lead to a mechanistic understanding **diffusion** based on the interaction of **individual molecules**.

Random walks and diffusion

More importantly:

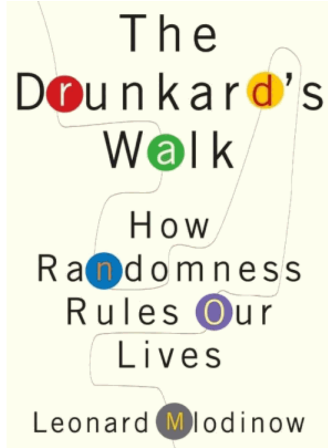
Shows how the kinematics of small scale motion leads directly to macroscale properties

Microscopic	Macroscopic
Random walk	Diffusion
Property of "individual"	Property of "population"

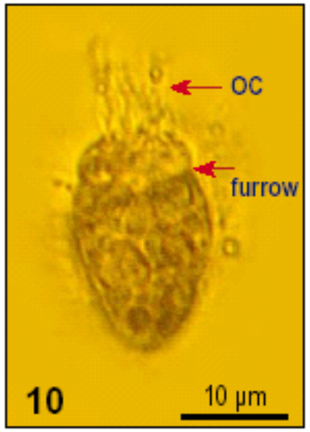
Molecular
Turbulence
Motility of organisms

Brownian motion

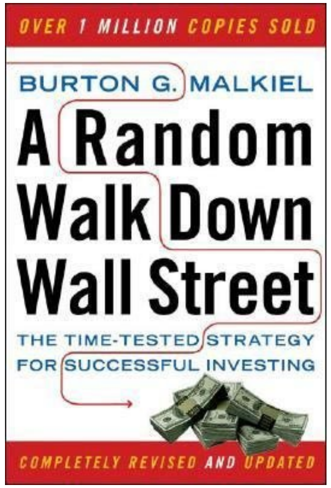
Brownian motion *per se*, has implications for
(1) The diffusion of molecules and ions in solution: e.g. nutrients, O_2, salt ions
(2) Directly effects the motion of small suspended particles
(3) Directly effects the motion of microbes: bacteria and viruses



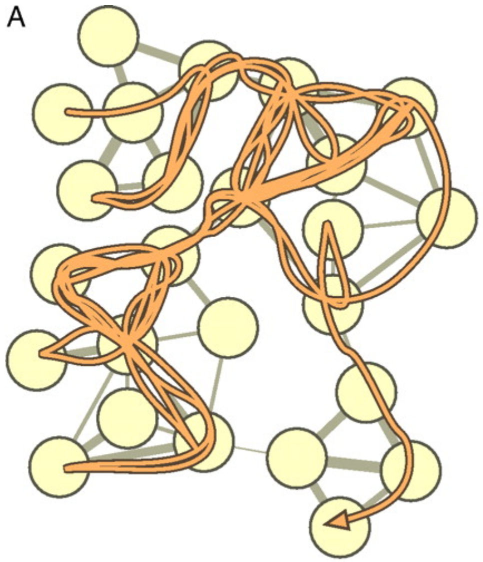
Brownian motion is also a good analogue for the random motility of larger self-propelled plankton such as ciliates, flagellates and copepods.

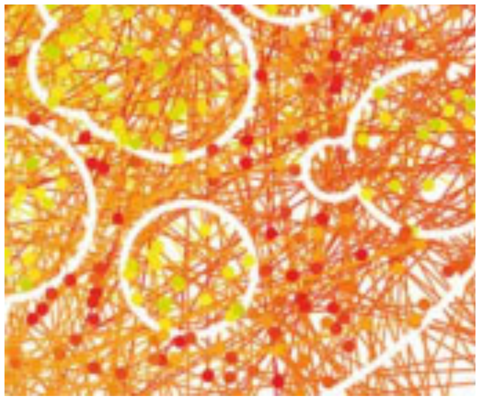


Found in many other branches of research
Evolution: random walk on a genome
Mathematics: Stochastic calculus
Economics: Scholes & Black

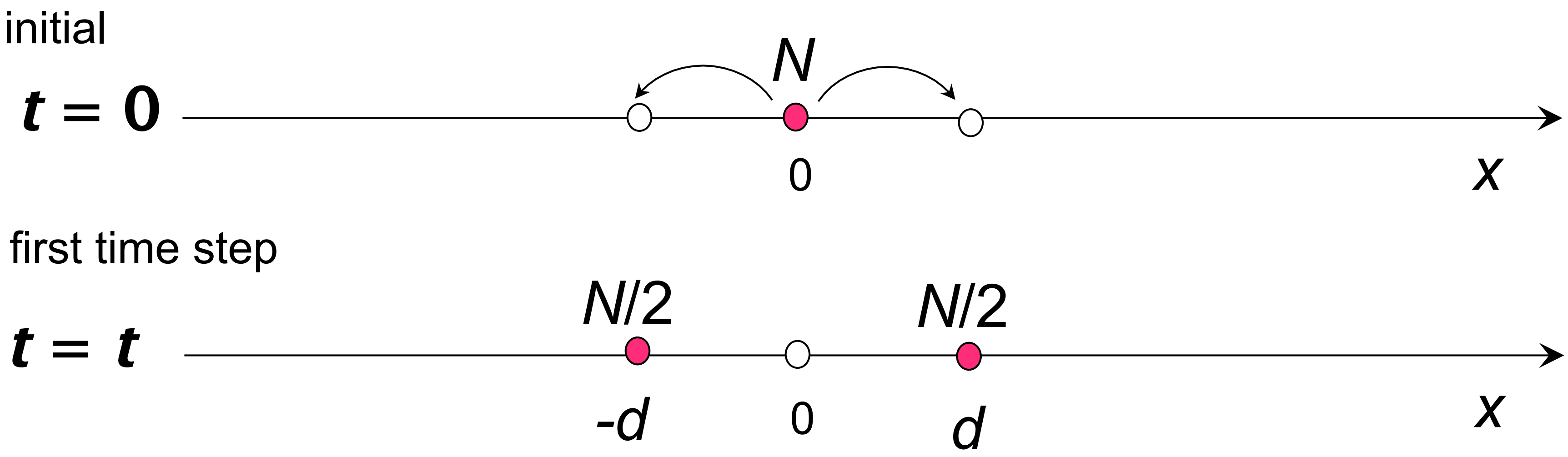


A





Diffusion as a random walk 1D



After n time steps: $t = nt$

Mean: $\langle x \rangle = 0$

Variance: $\langle x^2 \rangle = nd^2$

That is, the mean position remains the same while the variance increases linearly with time

This can be verified using a simple program

Diffusivity *is* the rate of change of variance

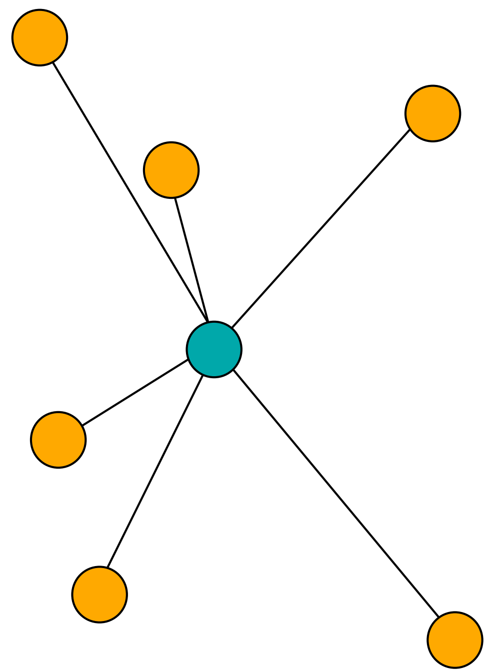
$$D = \frac{1}{2}\frac{d}{dt}\left\langle (x - \bar{x})^2 \right\rangle$$

For 1 dimension

mean position

$$D = \frac{1}{2N}\frac{d}{dt}\left\langle (x - \bar{x})^2 \right\rangle$$

For N dimensions



Recall for 1 D example:

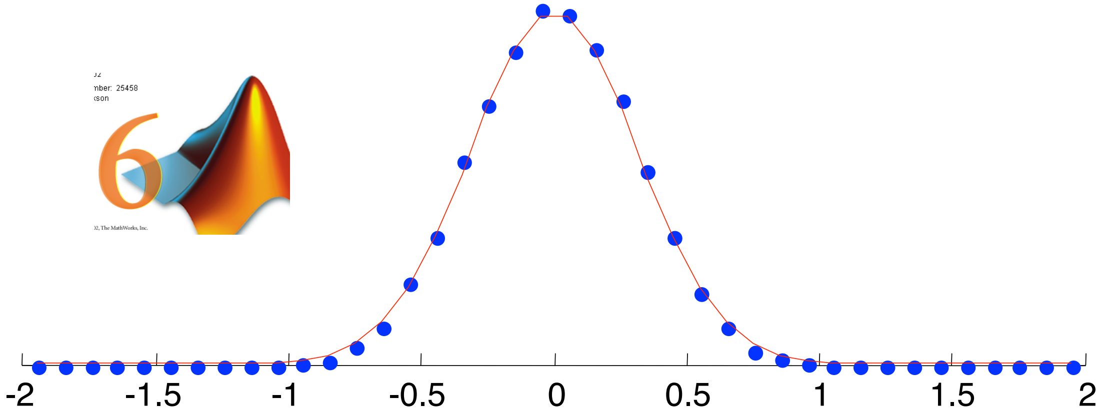
After n time steps: $t = nt$

Mean: $\langle x \rangle = 0$

Variance: $\left\langle x^2 \right\rangle = nd^2$

$$D = \frac{1}{2}\frac{d^2}{t}$$

Diffusion in 1D



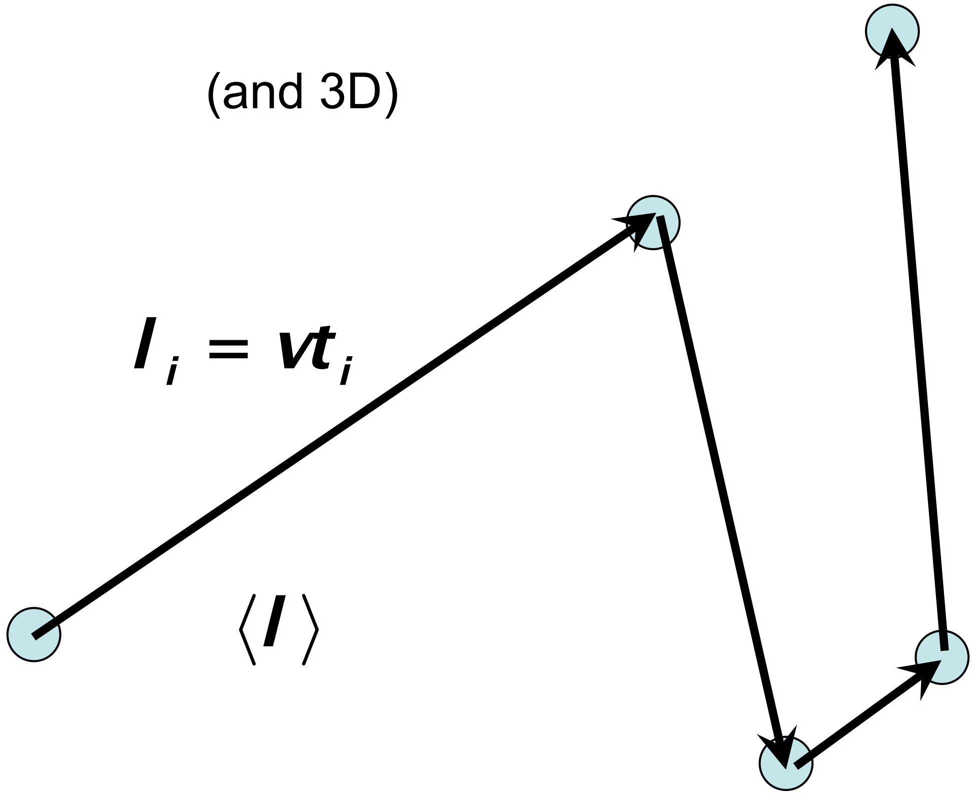
Under diffusivity D

$$p(x,t)\,dx\,dt = \frac{1}{\sqrt{4\pi D t}} \exp\left(\frac{-x^2}{4Dt}\right)$$

The probability of finding a particle that was initially ($t = 0$) at $x = 0$, in a small interval $[x \pm dx]$ in the time interval $[t \pm dt]$

Random walk 2D

(and 3D)



Simplest model

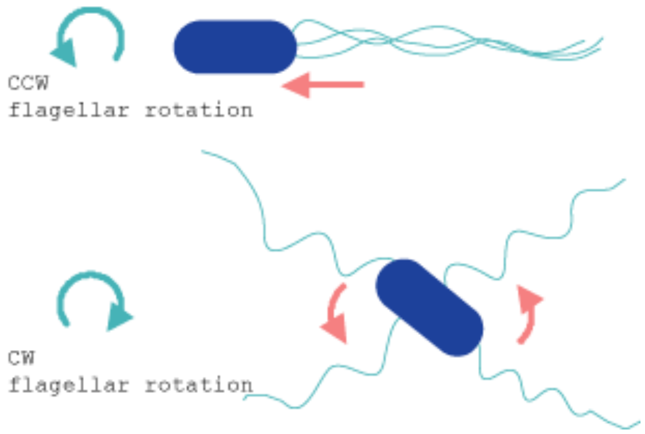
Organism moves along a linear path at a constant speed for some time, after which it “tumbles” and proceeds in a new, random direction.

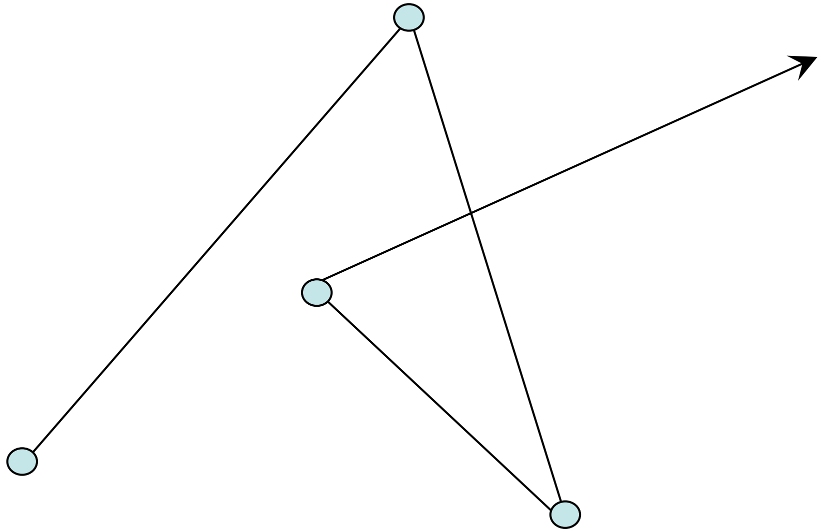
$$D = \frac{1}{4}\frac{\langle l^2 \rangle}{\langle t \rangle} = \frac{1}{4}\frac{\langle (vt)^2 \rangle}{\langle t \rangle}$$

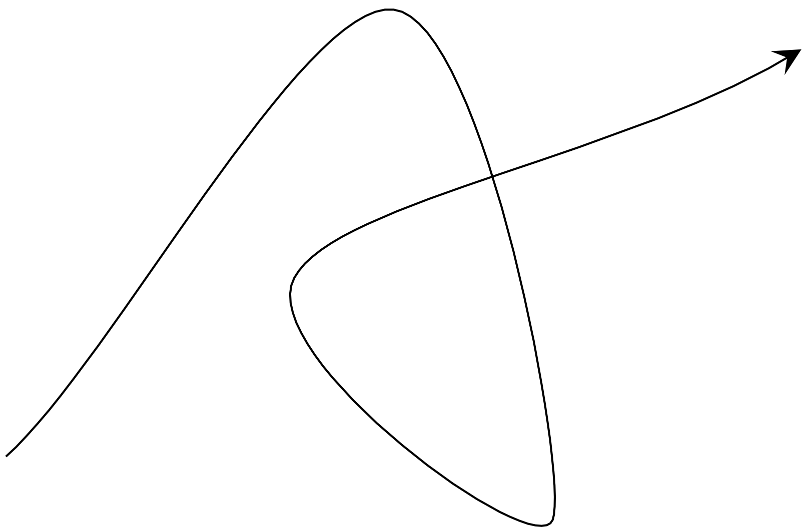
Depends on statistics of tumbles

Tumble interval uniform, then $D = \frac{1}{4}vt$	Tumble interval exponentially distributed then $D = \frac{1}{2}vt$

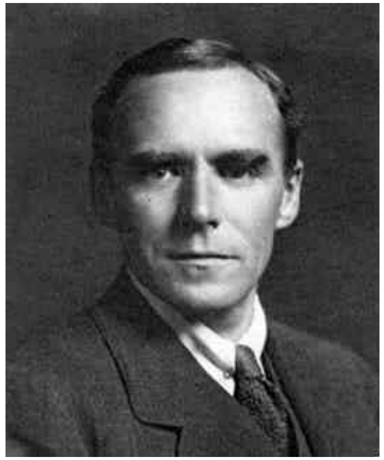
Run-tumble vrs smoothly continuous random walks







Diffusion by continuous motion



GI Taylor

G.I. Taylor (1921); Diffusion by continuous random (Brownian) motion

$$I^2 = 2l\left(L - l\left(1 - e^{-L/l}\right)\right)$$

Net displacement

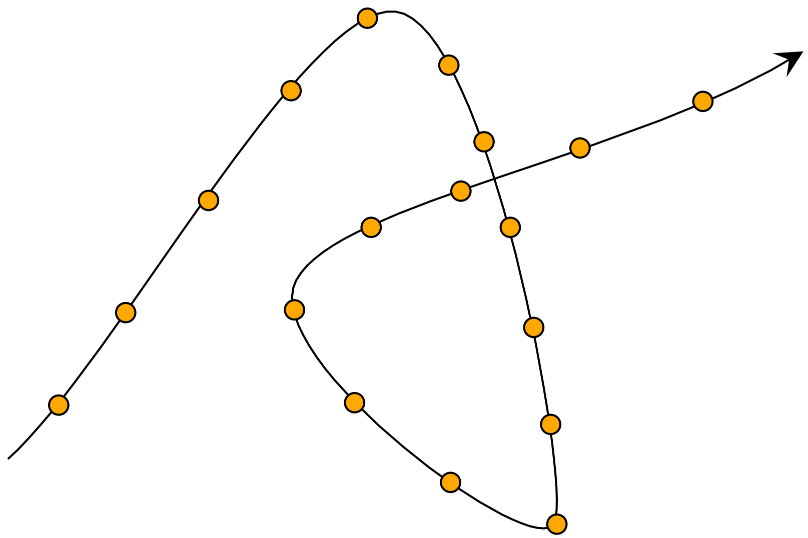
Correlation length scale

Gross displacement

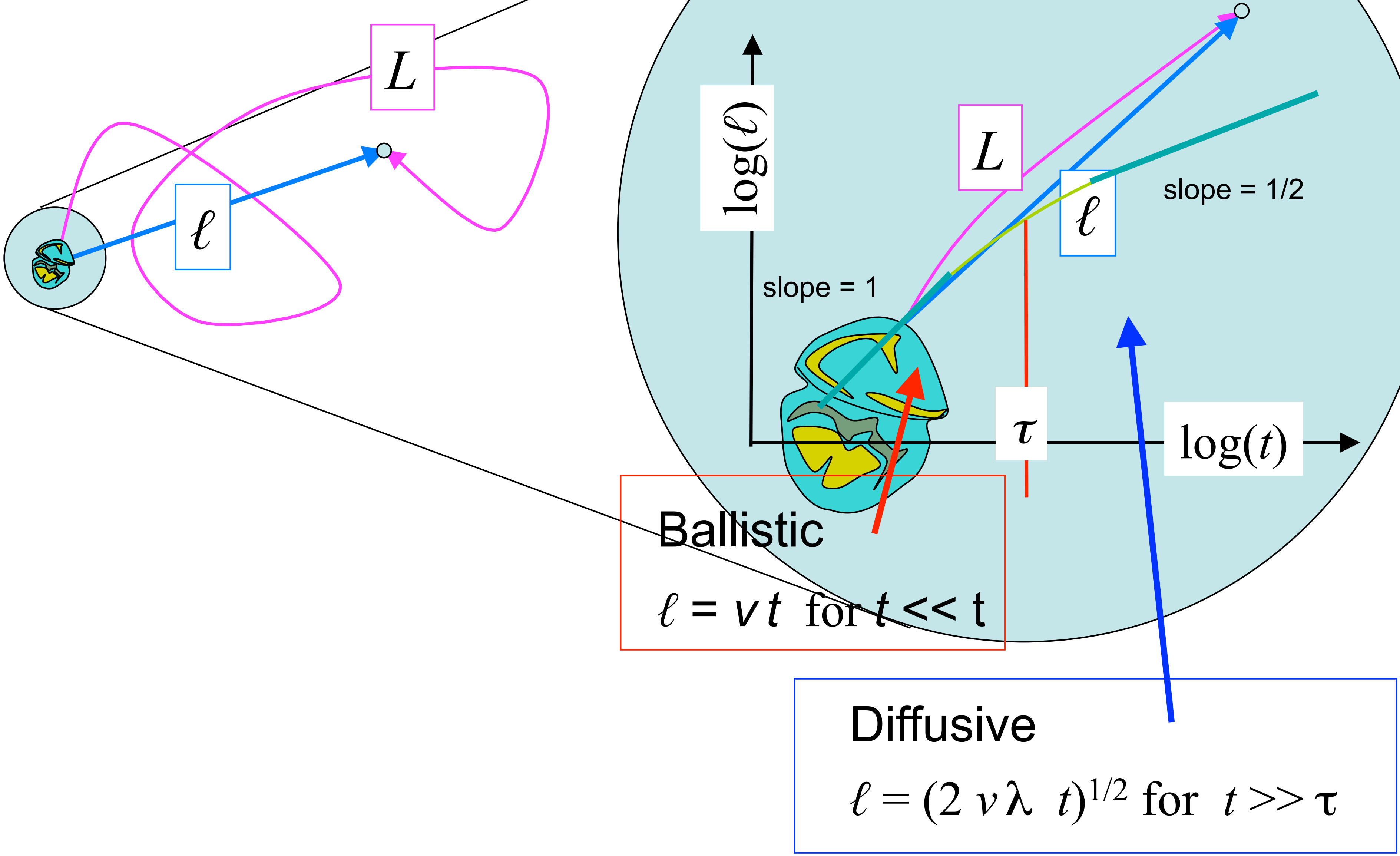
or equivalently

$$I^2 = 2u^2 t\left(t - t\left(1 - e^{-t/t}\right)\right)$$

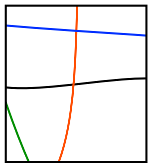
Correlation time scale



Diffusion by continuous motion

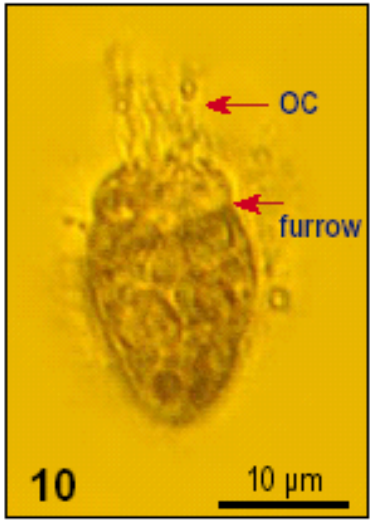


Diffusion by continuous motion



Diffusion by continuous motion

Example

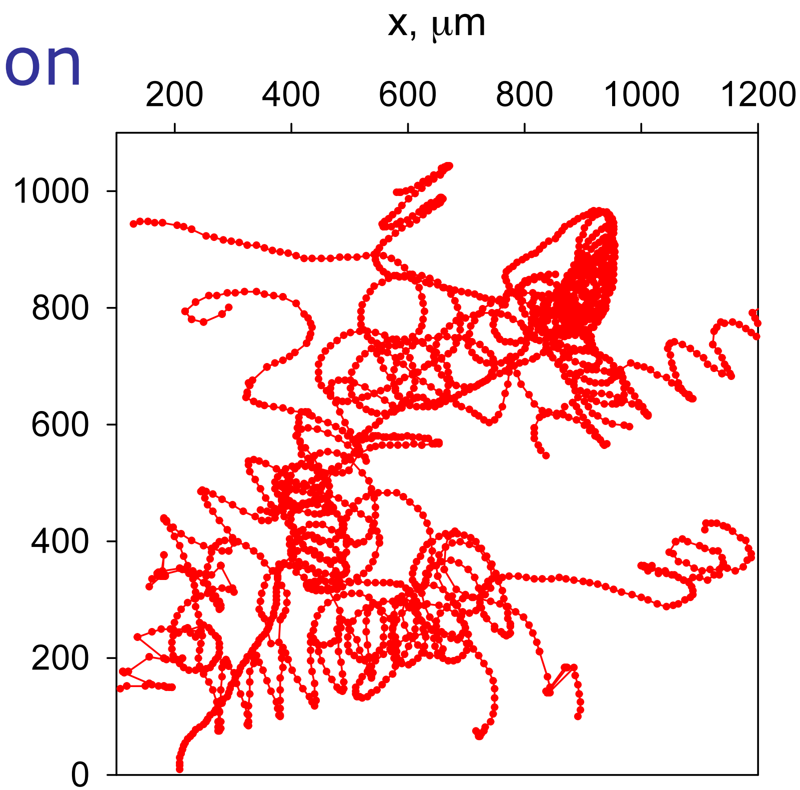


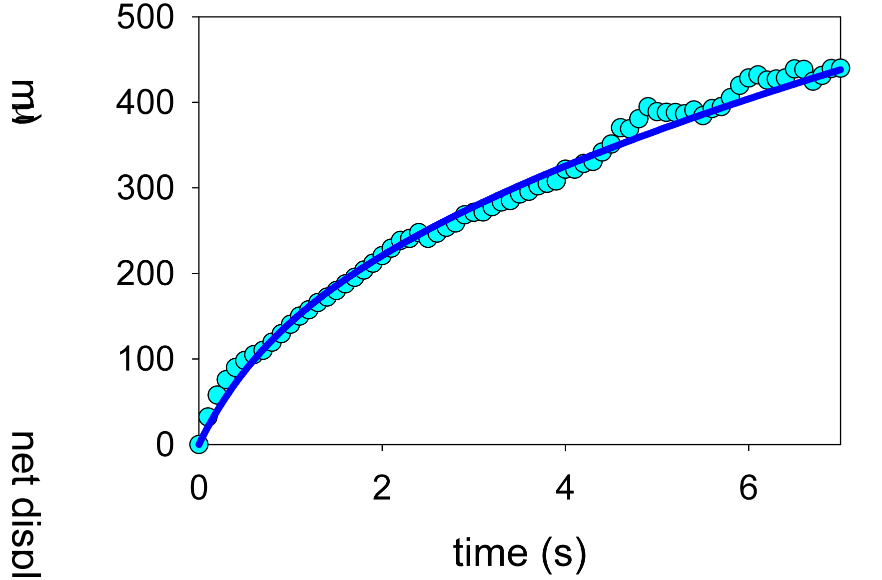
Ciliate *Balanion comatum*

v = 220 ± 10 μm/s
τ = 0.3 ± 0.03 s
λ = 65 ± 10 μm
D = 50 ± 10 x 10^{-6} cm^2/s

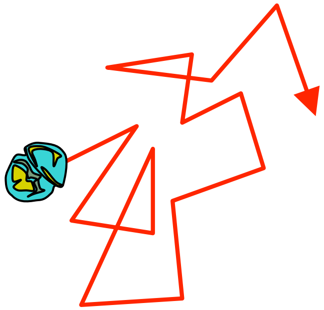
similar motility for organisms from bacteria to copepods

Jakobsen et al (2007)
Visser & Kiørboe (2006)

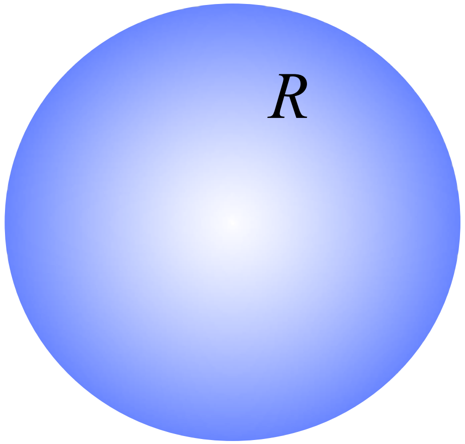




Diffusive model



Random walk diffusion



$$D = \frac{v\lambda}{3}$$

Diffusion equation

$$\frac{\partial c}{\partial t} = \frac{1}{r^2}\frac{\partial}{\partial r}\left(r^2 D \frac{\partial c}{\partial r}\right)$$

$$c(R) = 0,\; c(r\rightarrow\infty) = C$$

Encounter rate:

$$Z(t) = -\oint_S D \frac{\partial c}{\partial r}\hat{r}\cdot d\hat{s}$$

time dependent

$$Z(t) = \frac{4}{3}\pi C R v\lambda\left(1 + \sqrt{\frac{3R^2}{\pi v\lambda t}}\right)$$

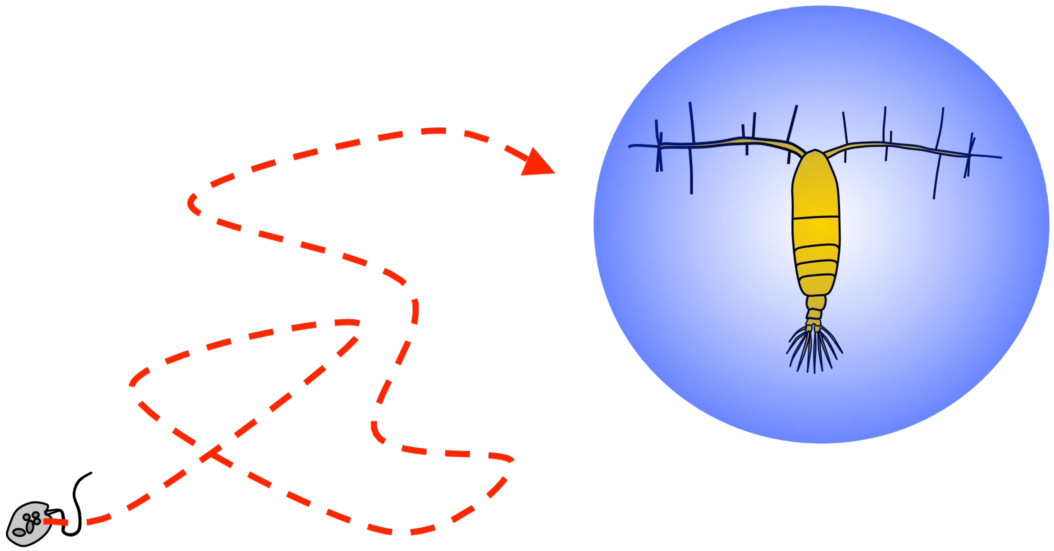
steady state

$$Z(t\rightarrow\infty) = {}^{4}/_{3}\; C\,\pi\, R\, v\, \lambda$$

What does this mean for encounter rates ?

simple example

Ambush predator feeding on motile prey



Motility length scale λ

Capture radius R

Swimming speed v

Two encounter rate models !!

Two encounter rate models

Ballistic $Z = C pR^2 v$

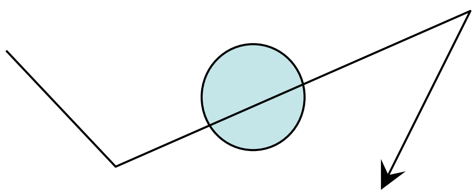
Diffusive $Z = \frac{4}{3} pCRvl$

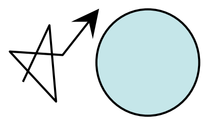
Which one to use??

Has to do with the relative size of *l* and *R*

$R < l$ ballistic

$R > l$ diffusive

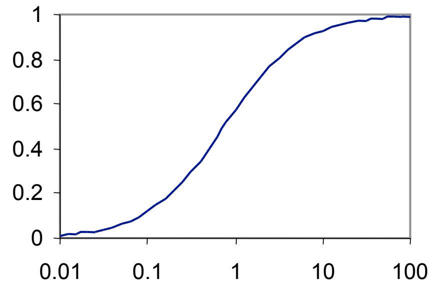


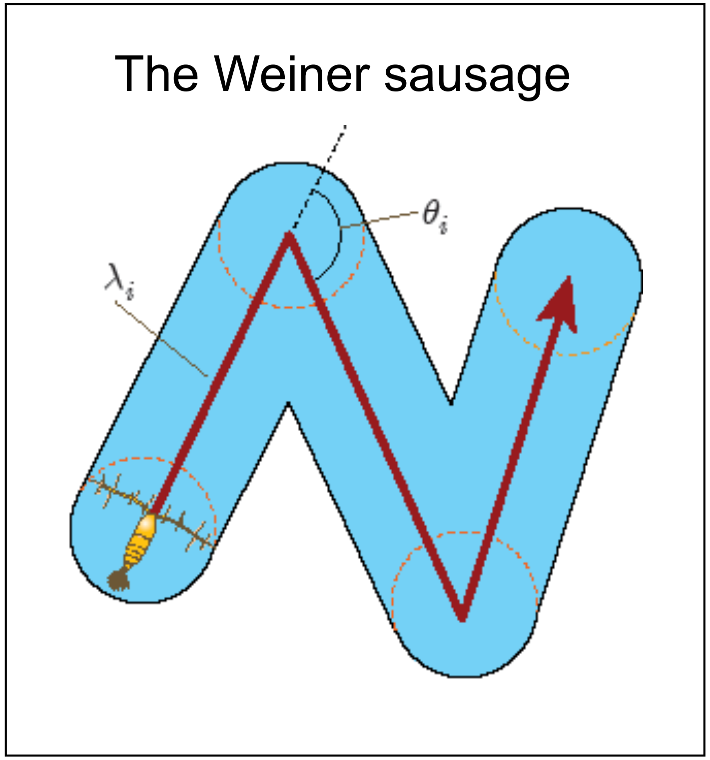


Ballisto-diffusive encounter rates

We can combine both estimates into 1 expression, covering both limiting cases as well as the transition:

$$Z = \frac{4l}{4l + 3R} C p R^2 v$$



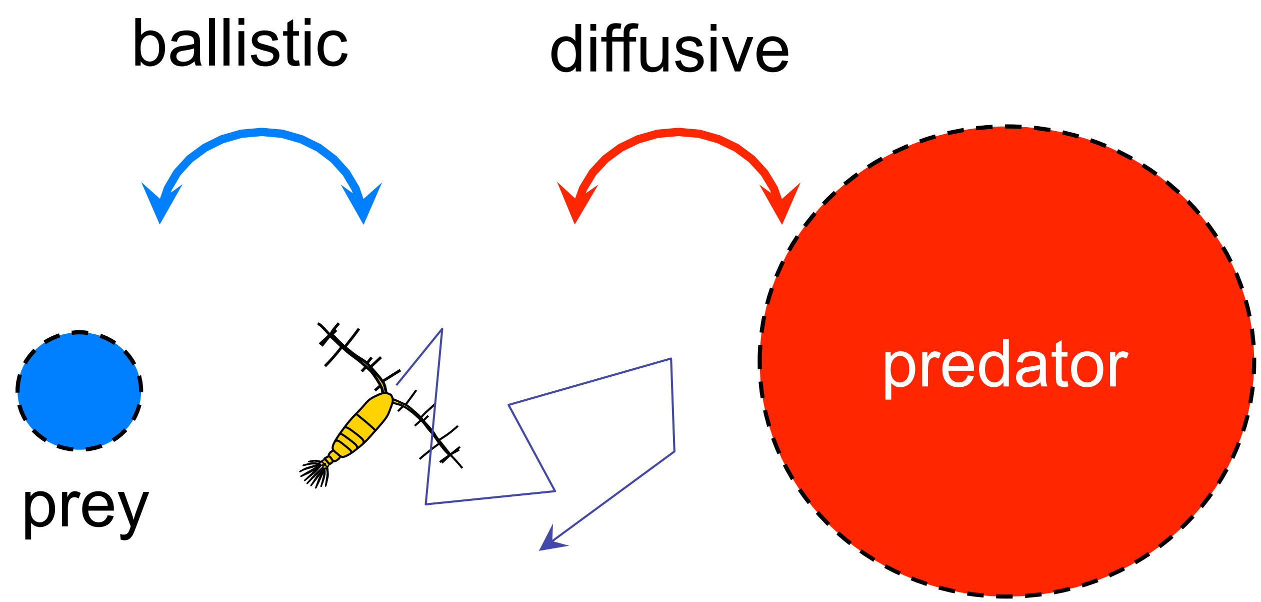


Maximized when $l > R$ (ballistic)

…and becomes smaller for $l < R$ (diffusive)

Implications for the behaviour of zooplankton

Is there an optimal behaviour for organisms ?



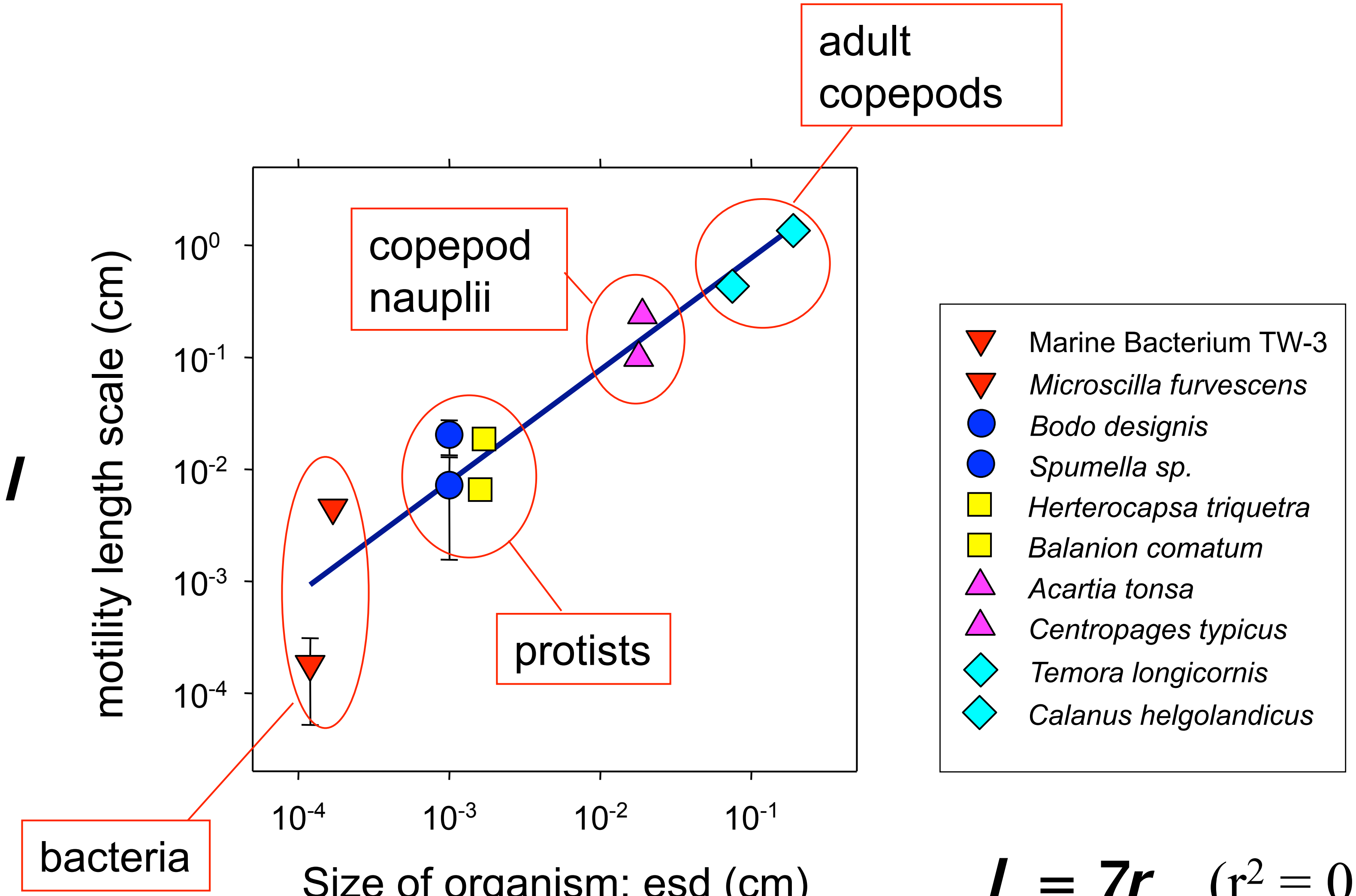
predator to prey scaling ≈ 10:1

R_{prey} < mean path length < $R_{predator}$

An organism of size r, detects its prey at about the same scale ($R_{prey} \approx r$), and is in turn detected by its predator at about 10 times this distance ($R_{preadtor} \approx 10\ r$).

That is, an organism of size r should choose its motility length scale to lie between r and $10\ r$.

Motility length vrs body size



$$l = 7r \quad (r^2 = 0.90)$$