TRAIT BASED ZOOPLANKTON ECOLOGY

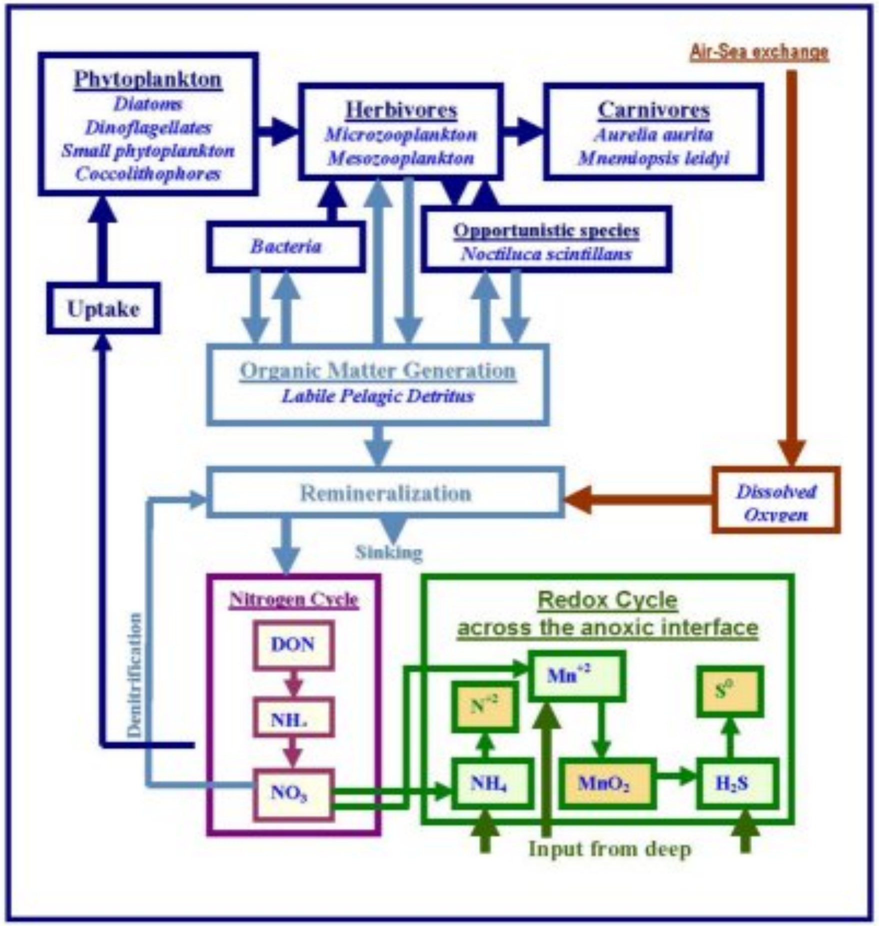
Build your own animal

SloMo: 140x

Thomas Kiørboe

Technical University of Denmark

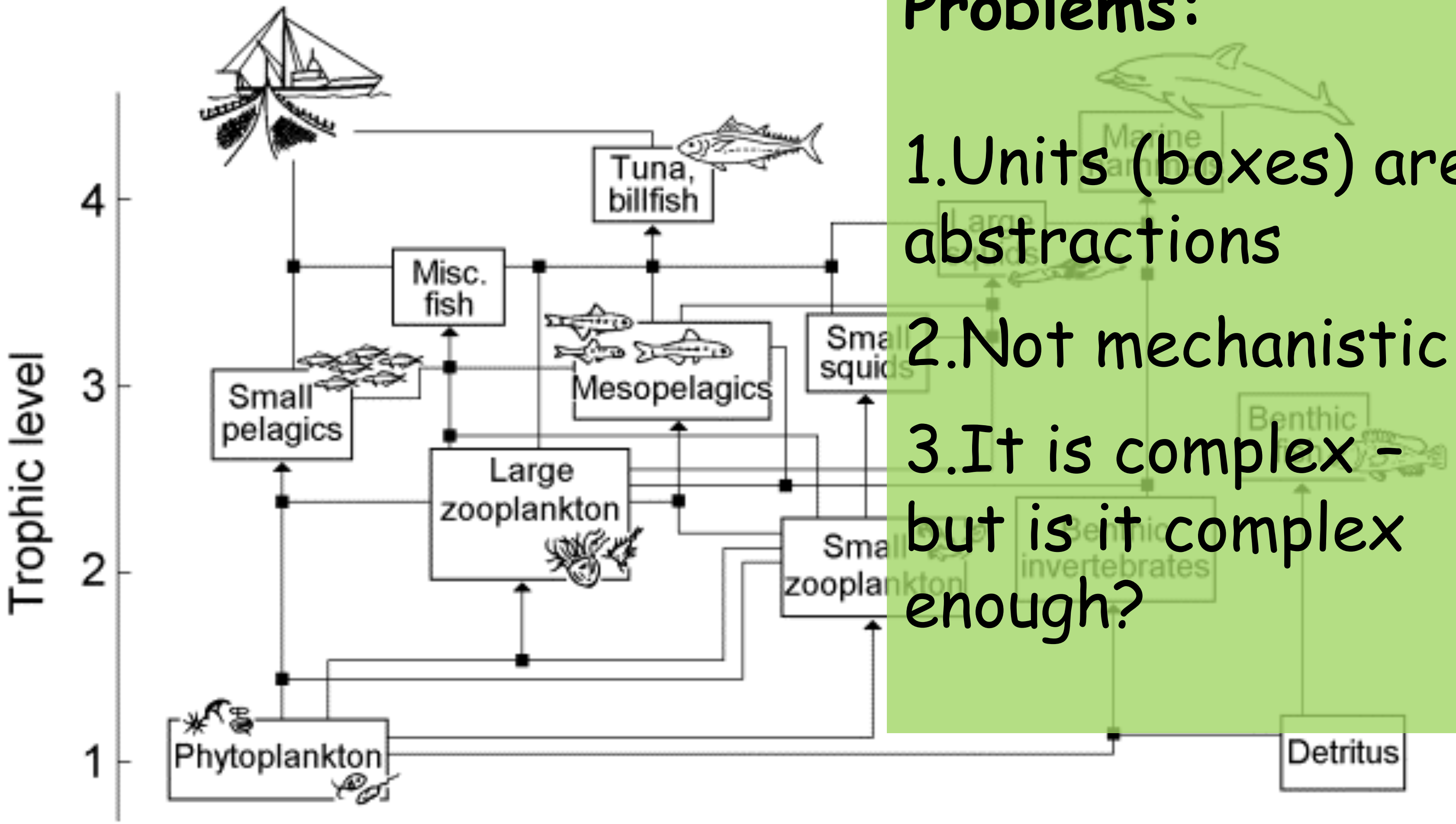
Schematic of pelagic food web



Problems:

1. Units (boxes) are abstractions
2. Not mechanistic
3. It is complex – but is it complex enough?

Schematic of pelagic food web



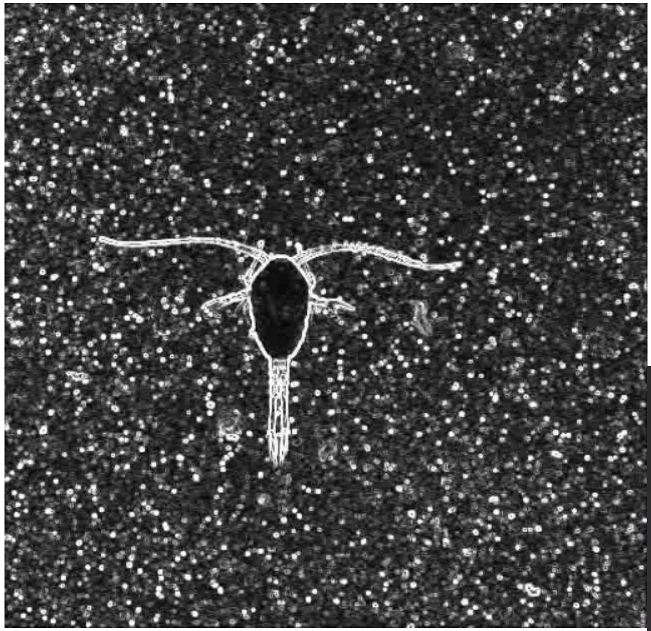
Problems:

1. Units (boxes) are abstractions
2. Not mechanistic
3. It is complex - but is it complex enough?

Trait based models

- Replace species with individuals
- Individuals characterized by few *fundamental traits*
- Mechanistic description of traits
- Quantification of trade-offs
- Fitnes optimization
- Ecosystem structure and function emerge

Fundamental activities



Feed

Survive

Reproduce

Challenges to planktonic life

- 3-dimensional environment.
- Viscous
- Vision plays (almost) no role

Trade offs

There are **conflicts** between the fundamental activities:

Feeding: predation risk, energy, time

Surviving: reduced feeding

Reproduction: predation risk, energy, time

Fitnes

Fitnes = f(feeding, survival, reproduction)

$$\sim \frac{\text{Gain}}{\text{Cost}}$$

Outline

- **The traits**:

  Mechanistic description of principal mechanisms of **feeding**, **surviving**, and **reproducing** in zooplankton

- **The trade offs**:

  Conflicting interests: interference between feeding, reproduction, and surviuval

- **Trait-based modelling:**

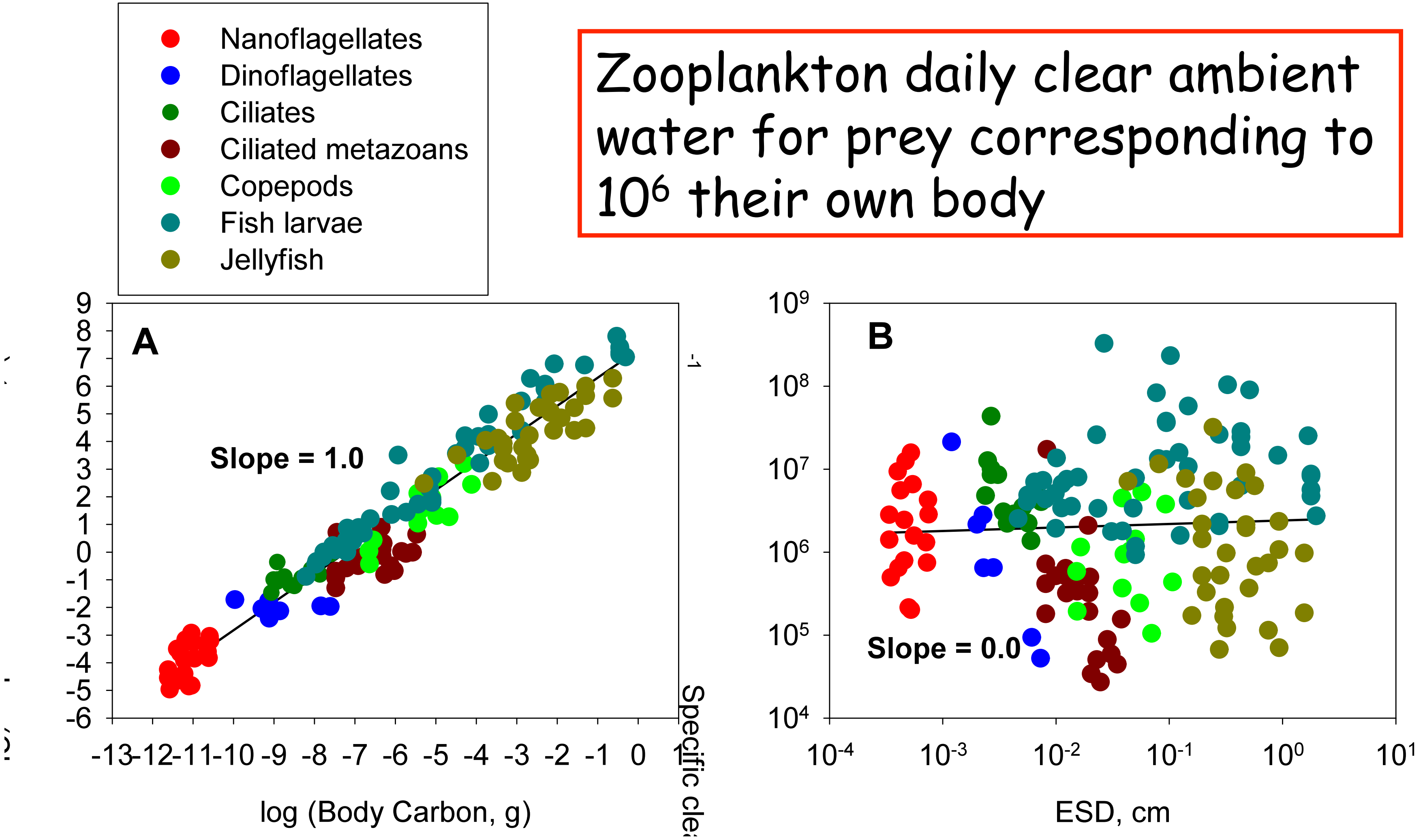
  A simple example of how system properties emerge from individual traits through fitness optimization

I. THE TRAITS:

1. Feeding

Clearance rates

Zooplankton daily clear ambient water for prey corresponding to 10^6 their own body



Kiørboe Biol. Rev. 2010

Feeding in sticky water

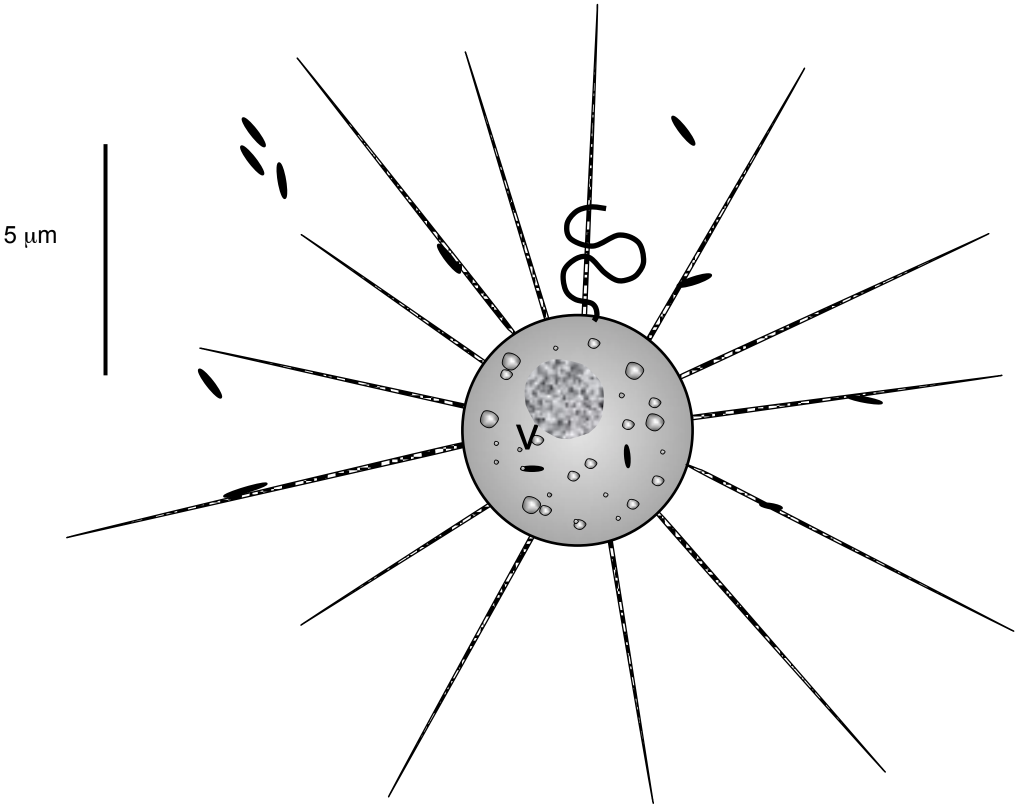
These are the challenges:

- The ocean is a **very** dilute suspension of food.
- Zooplankton must daily clear ambient water for prey corresponding to 10^6 their own body volume
- Water is very viscous at the scale of zooplankton

4 principal mechanisms

- Passive ambush feeding
  - *Diffusion feeding*
  - *Ballistic feeding*
- Active ambush feeding
- Feeding current feeding
  - *Direct interception*
  - *Filter feeding*
  - *Scanning current*
- Cruise feeding
  - *Hunting small particles (vision)*
  - *Hunting large particles*

Diffusion feeding

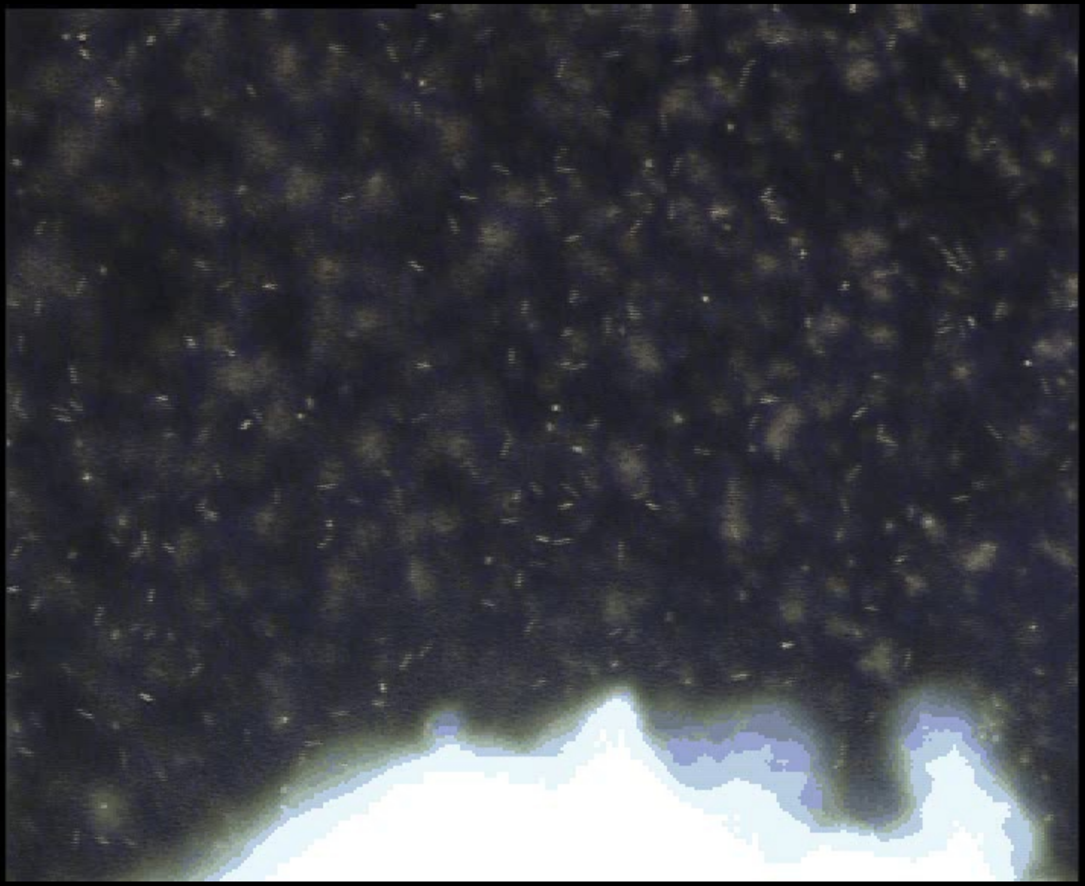


Helioflagellate
A large group of unicellular plankton feed on bacteria, that simply swim into the cell

Kiørboe 2008, *A mechanistic approach to plankton ecology*

Artwork by Sigrun Jonasdottir

Pelagic bacteria swim

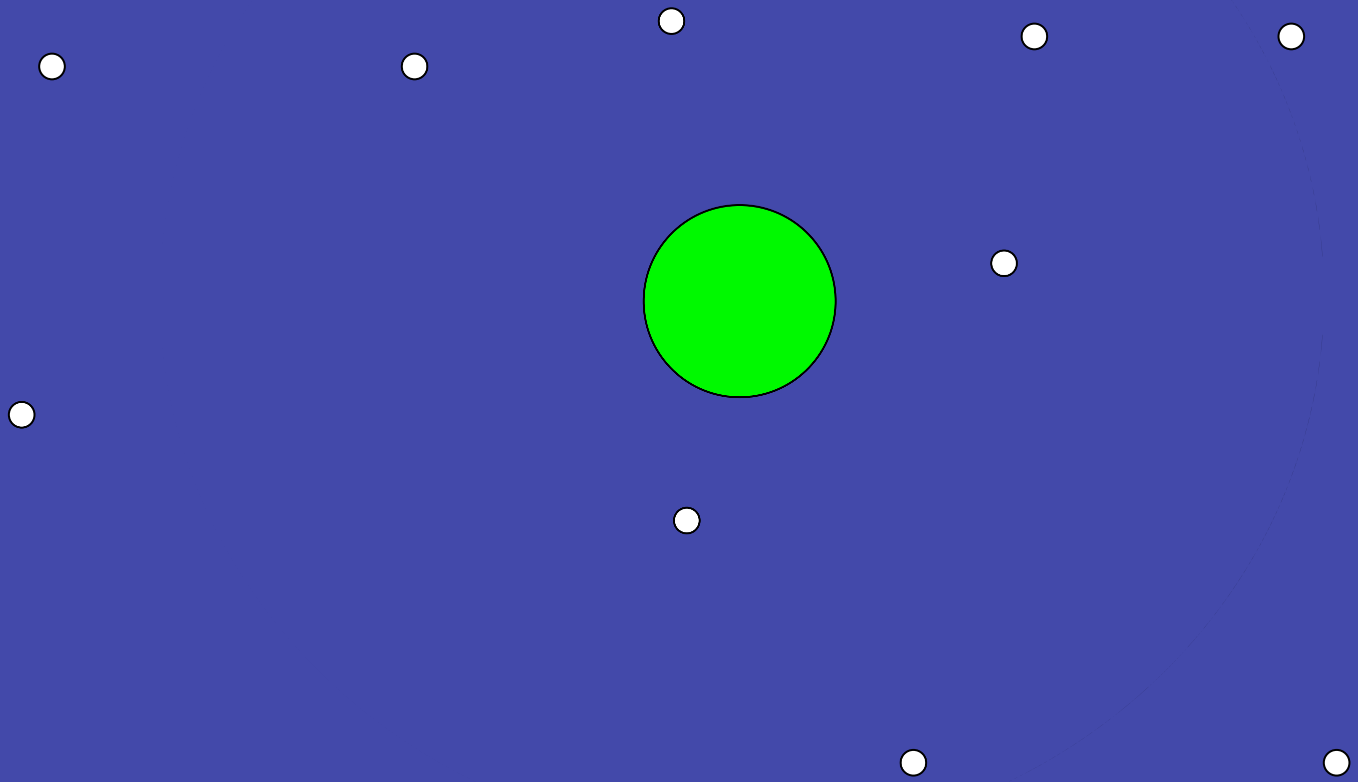


Pelagic bacteria swim

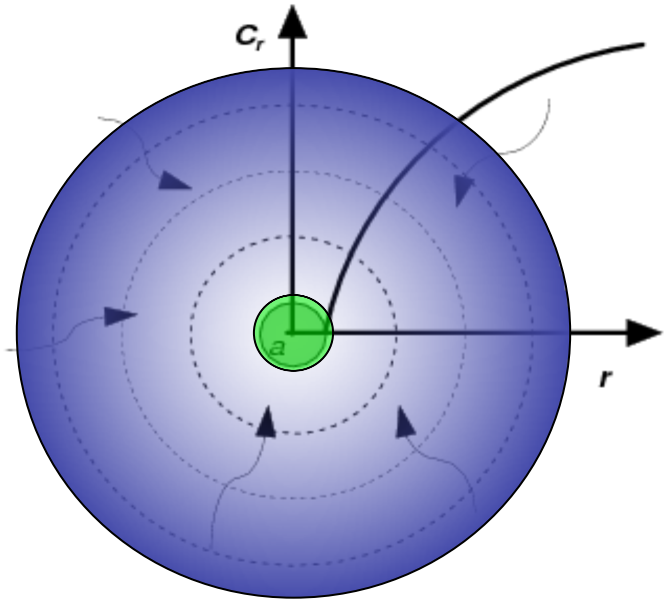
Their motility can be describe as a diffusion process with $D \sim 10^{-5}\ \mathrm{cm^2 s^{-1}}$

Kiørboe et al. AEM 2003

Diffusion feeding



Diffusion to absorbing sphere



Fick's 1st law:

$$J = -D\frac{dC}{dx}$$

$$Q = J4\pi r^2 = -D\frac{dC}{dr}4\pi r^2 = \boxed{-4\pi Da}C_\infty$$

Transport = Flux x Area

Clearance rate proportional to cell radius

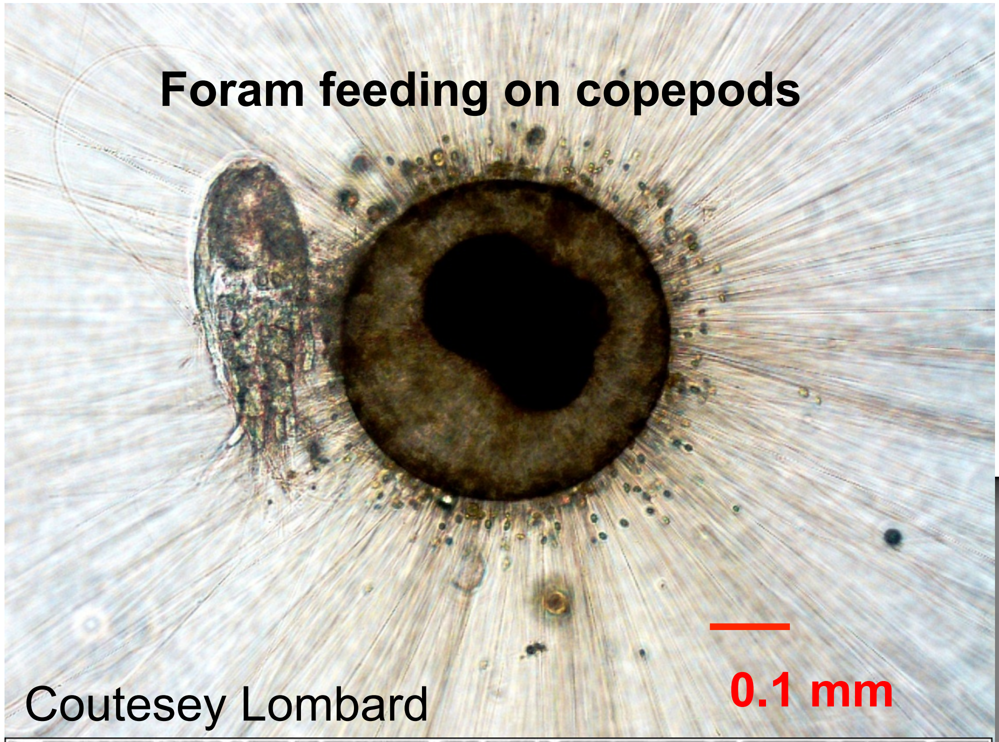
Specific clearance rate

Clearance rate per cell volumen:

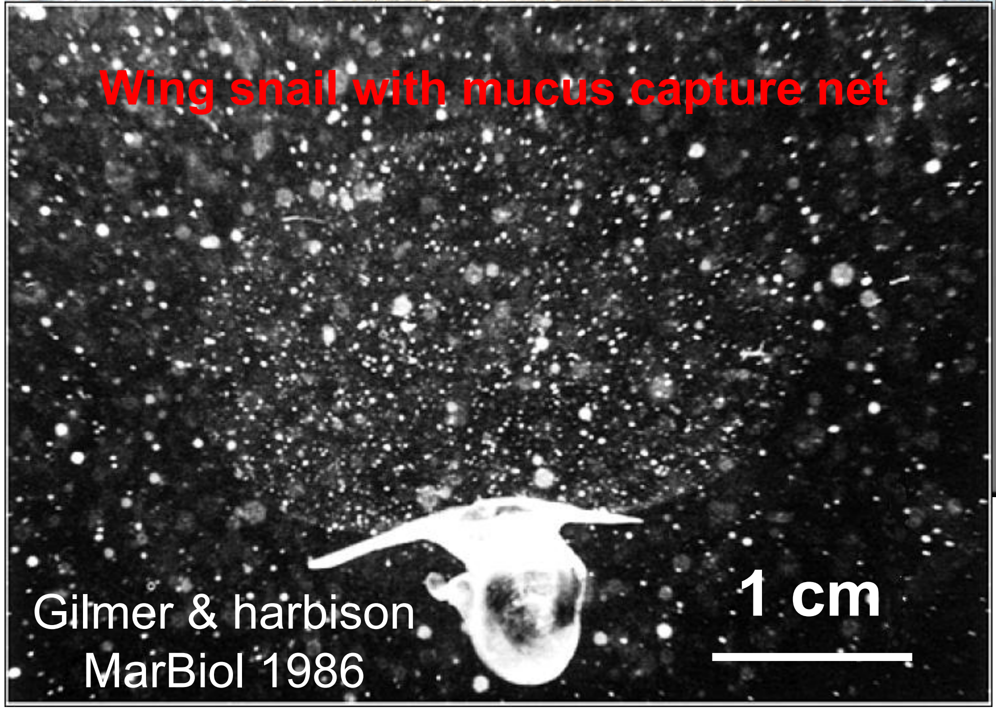
Diffusive prey motility

$$F' = \frac{F}{\frac{4}{3}\pi a^3} = -\frac{3DC_\infty}{a^2}$$

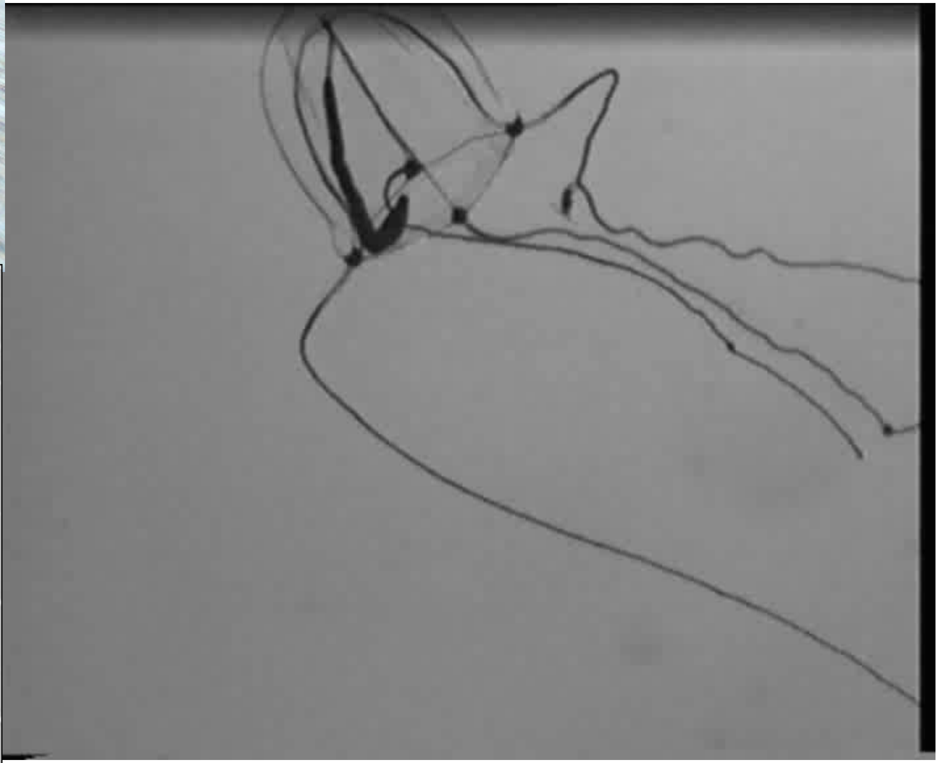
Diversity of passive ambush feeders


Foram feeding on copepods

Coutesey Lombard


Wing snail with mucus capture net

Gilmer & harbison
MarBiol 1986


Hydromedusa

Hanson & Kiørboe L&O 2005

4 solutions

- Passive ambush feeding
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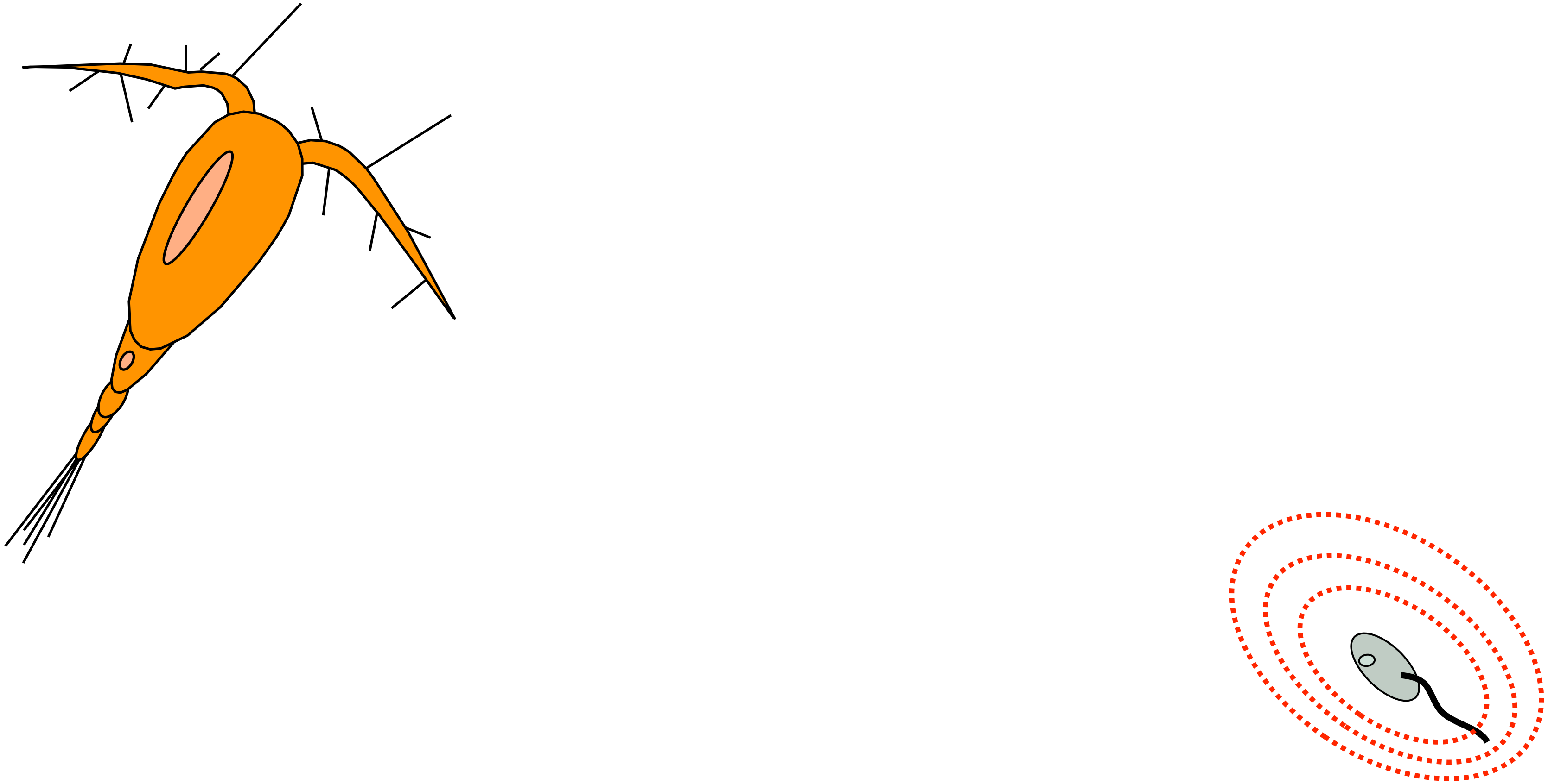
  - Ballistic feeding
- **Active ambush feeding**
- Feeding current feeding
  - Direct interception
  - Filter feeding
  - Scanning current
- Cruise feeding
  - Hunting small particles (vision)
  - Hunting larege particles

Active ambush feeding: remote detection and active attack

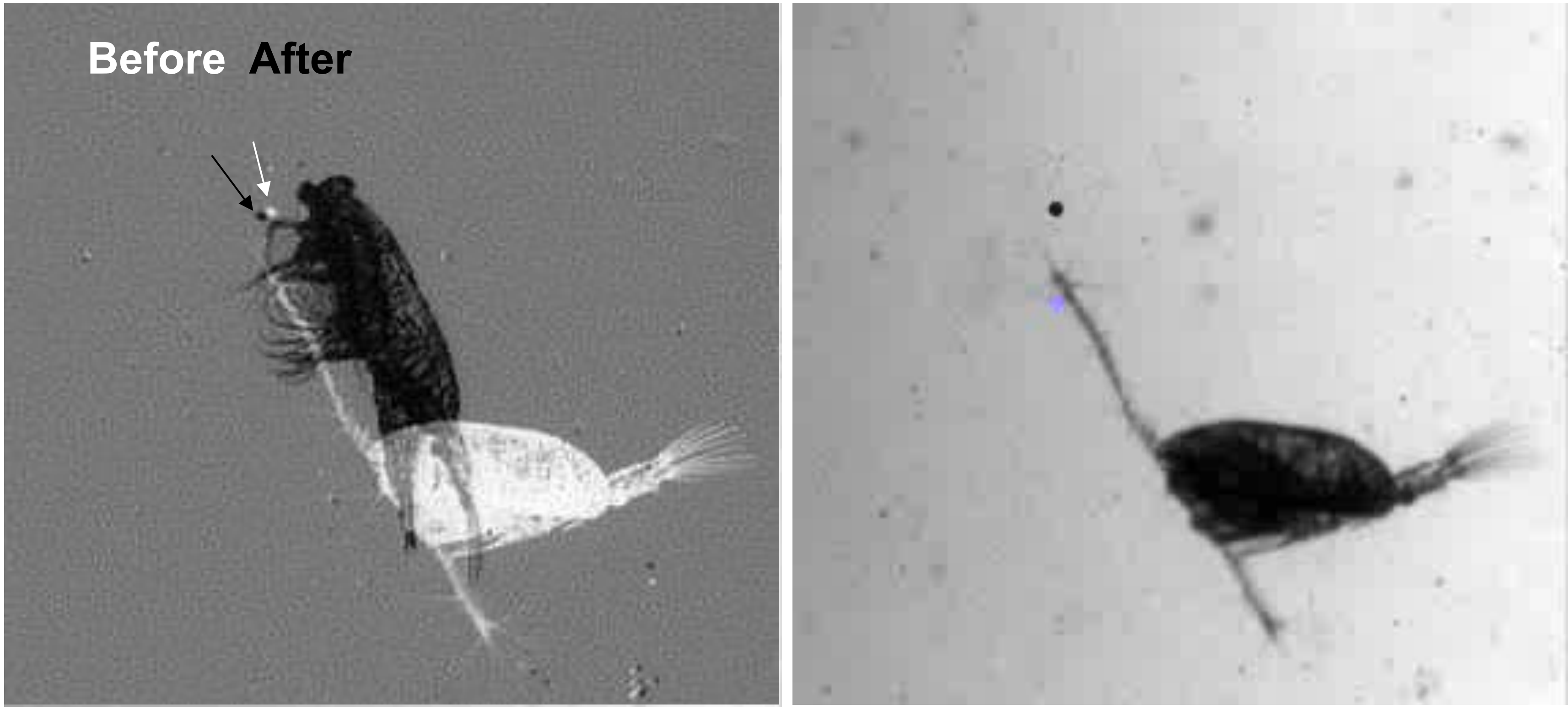


Prey attack in ambush feeding copepods

Real time

Slo mo

271 xReal time



Acartia tonsa

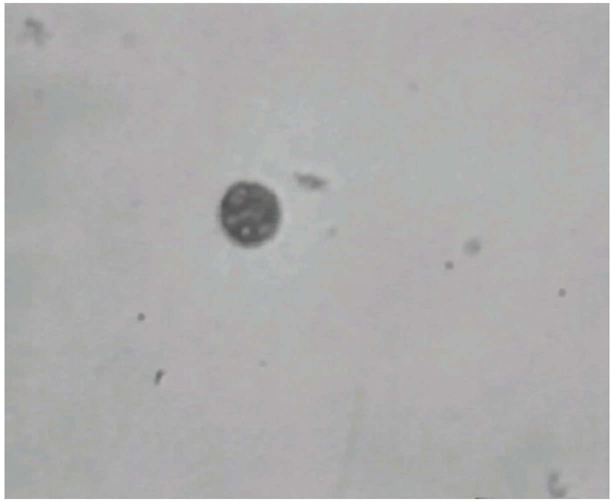
Duration of attack: 4 ms
Attack speed: 100 mm/s

1 mm

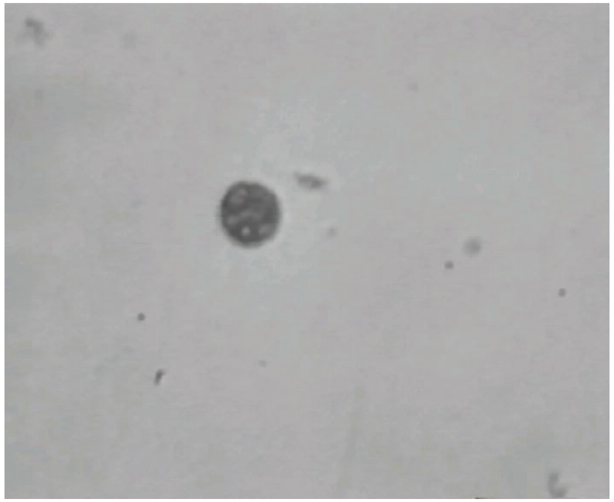
Kiørboe et al. PNAS 2009

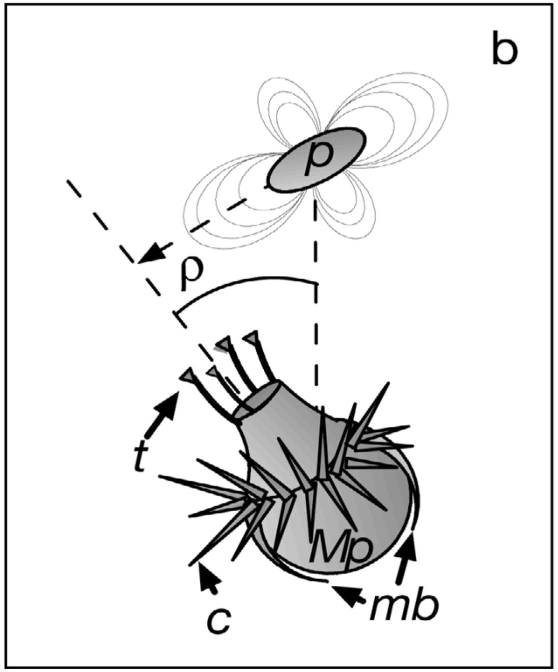
Ciliate feeding on dinoflagellate

Real time



Slo mo





Jakobsen et al. AME 2006

100 µm

4 solutions

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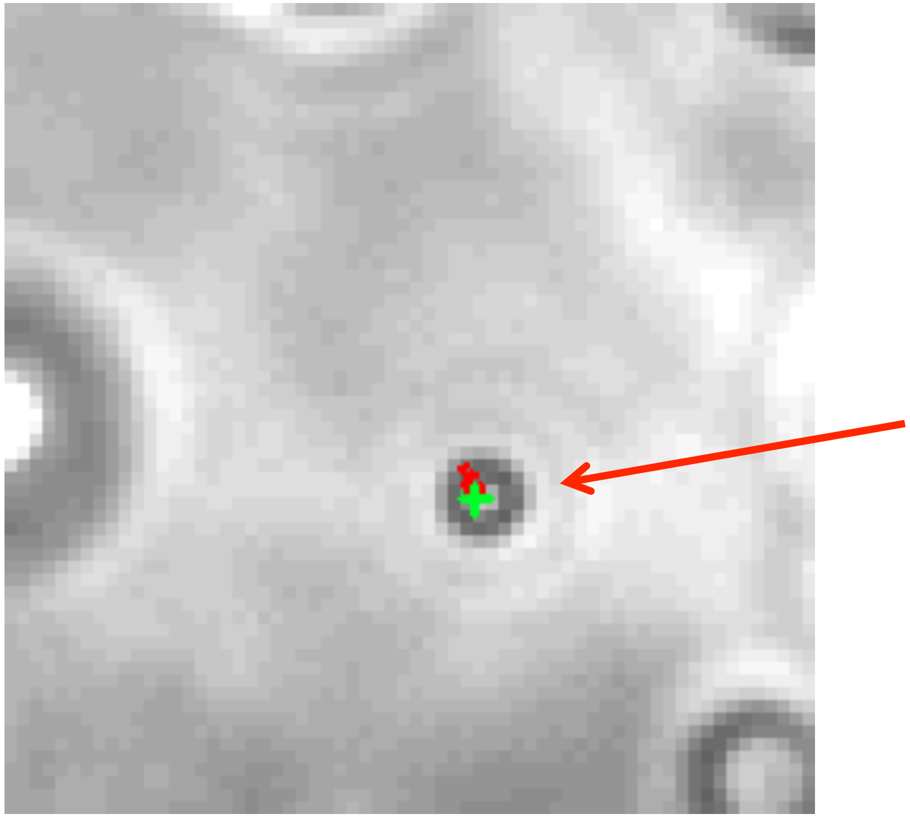
Fluid flow and interception feeding in nano-flagellates

Paraphysomonas sp
An interception-feeding flagellate

- Unicellular flagellates swim by means of one or two flagellae
- The swimming current is normally considered also to be a feeding current, also in *interception feeding* flagellates

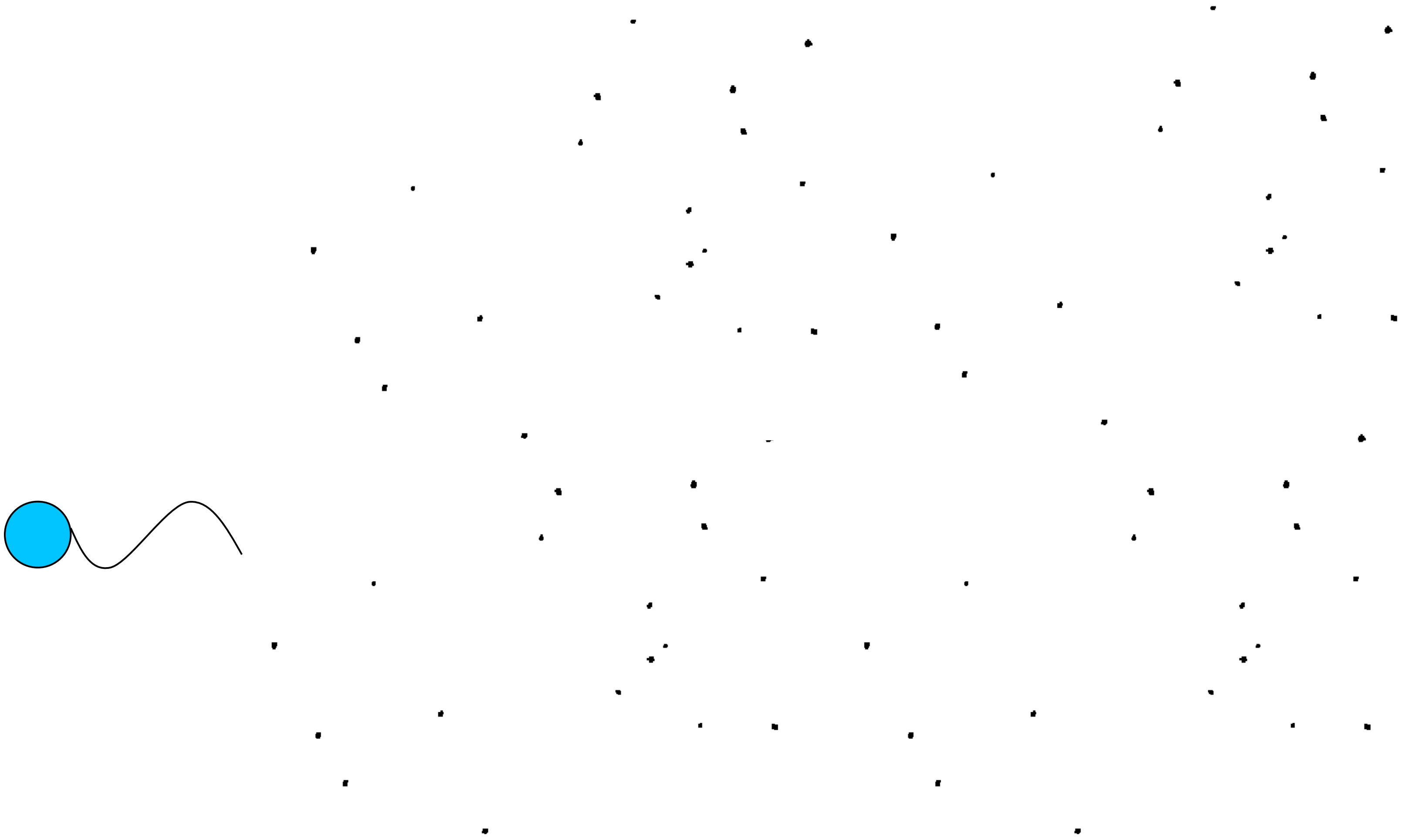
Problem: the viscous boundary layer pushes the prey away



Courtesey
Ray Goldstein

Slow motion

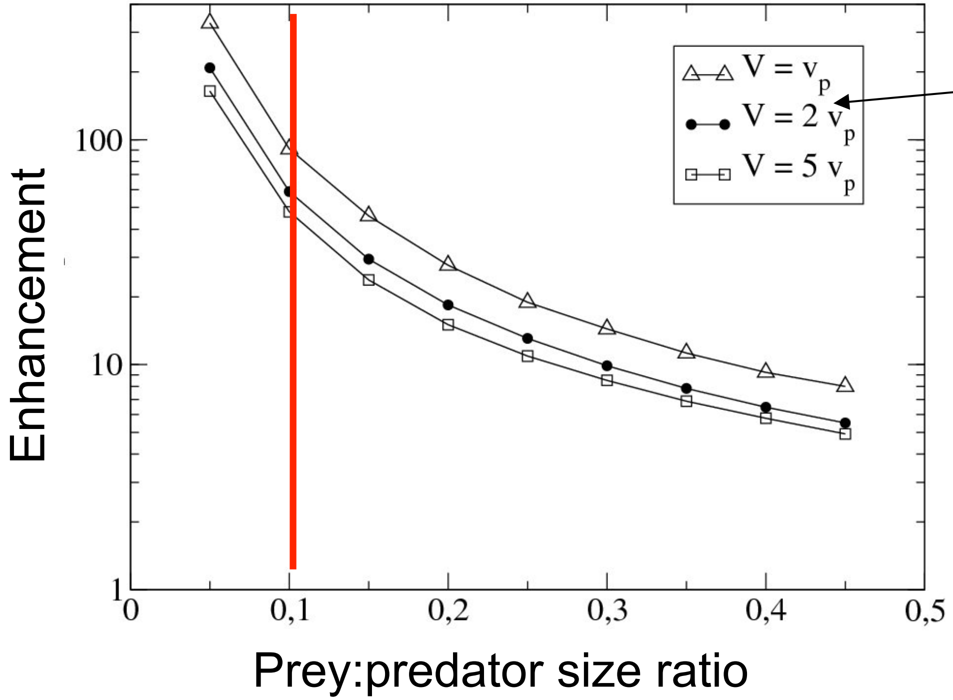
Bacteria prey move, however



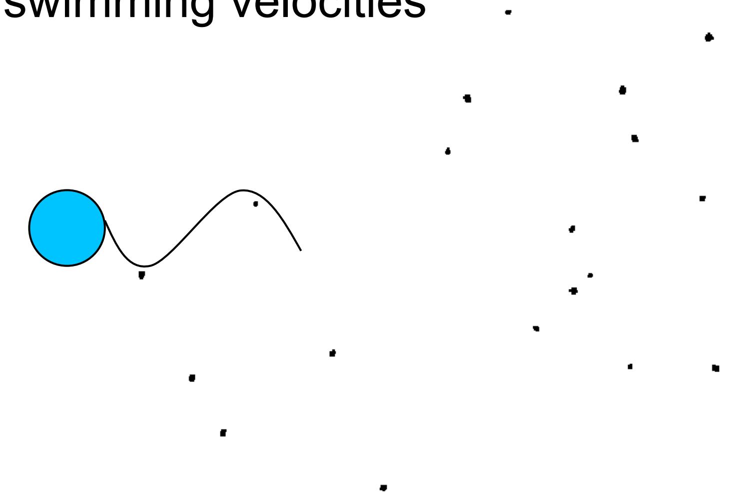
How does this affect the clearance rate of the flagellate?

Prey motility MUCH more important than feeding current

Enhancement of feeding on motile over non-motile prey



Relative prey swimming velocities



1. Consistent with clearance on dead and live bacteria
2. Hence, interception feeders swim to swim, not to feed

Langlois et al. AME 2009

4 solutions

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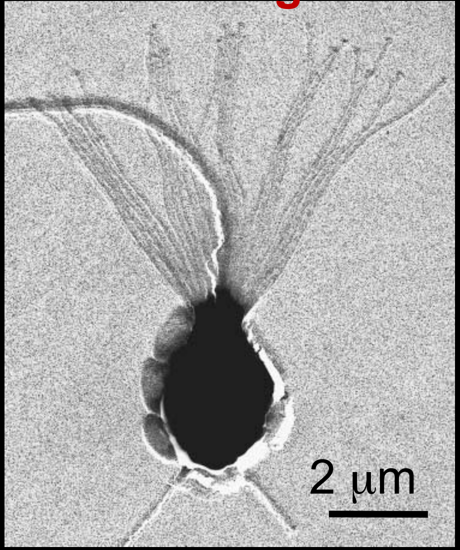
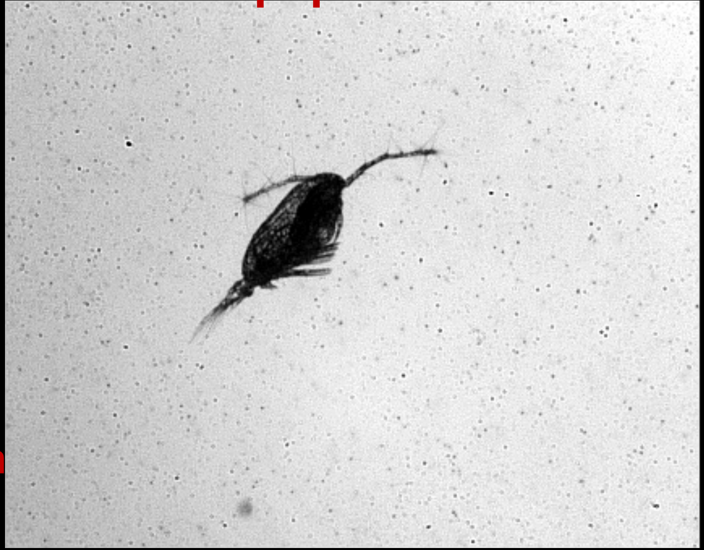
Filter feeders

Choanoflagellate



Copepod



0.5 mm

Apendicularian

0.5 mm

Doliolid

1 mm

4 solutions

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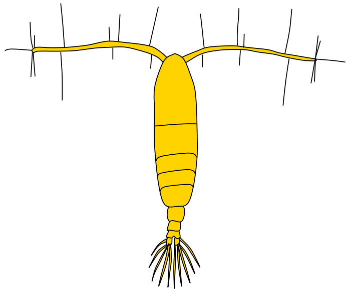
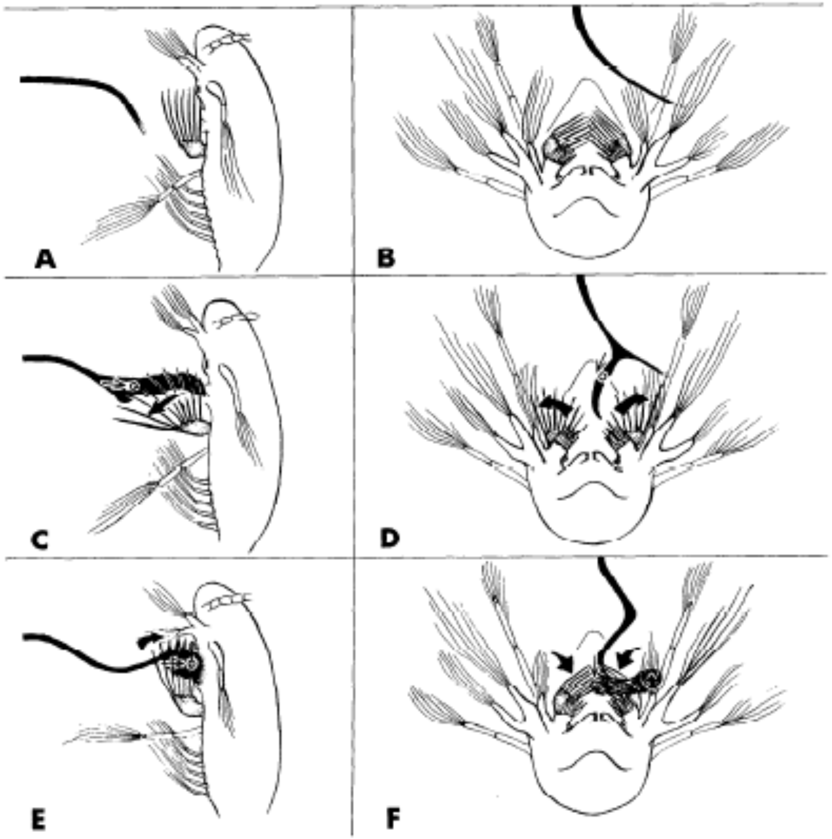
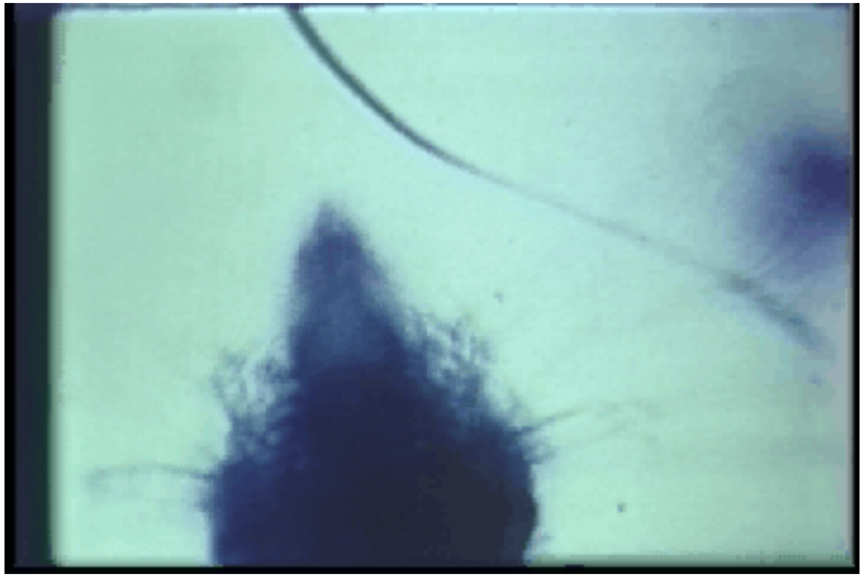


Scanning current





Redirection of scanning current

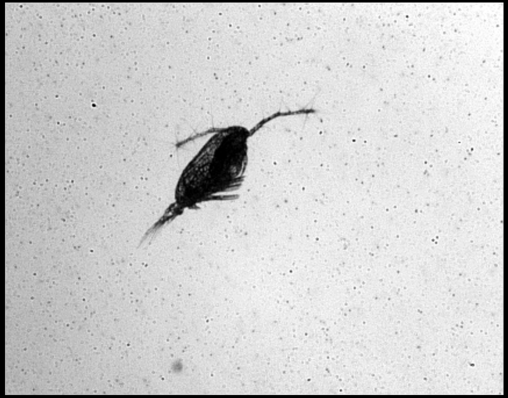
Koehl & Strickler L&O 1981

Hovering

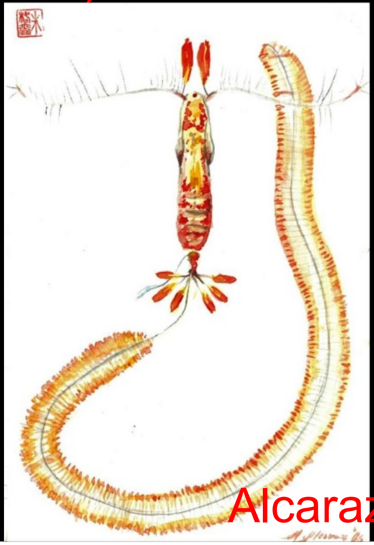
Acartia tonsa
Feeding bouts
(slo mo)

Pseudocalanus elongatus
Continous feeding current
(real time)

Temora longicornis
Continous feeding current
(slo mo)



Courtesey of Fenchel



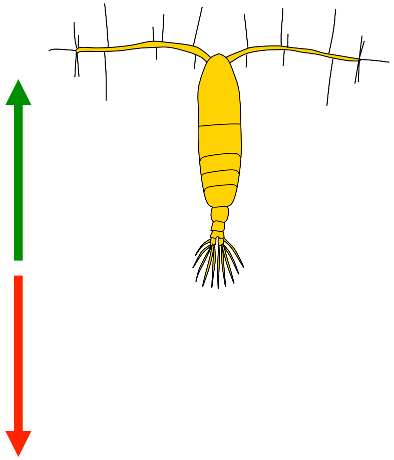
Alcaraz fecit

Cruising

Temora longicornis

Hovering or cruising?

Tethered copepod
(Hovering)



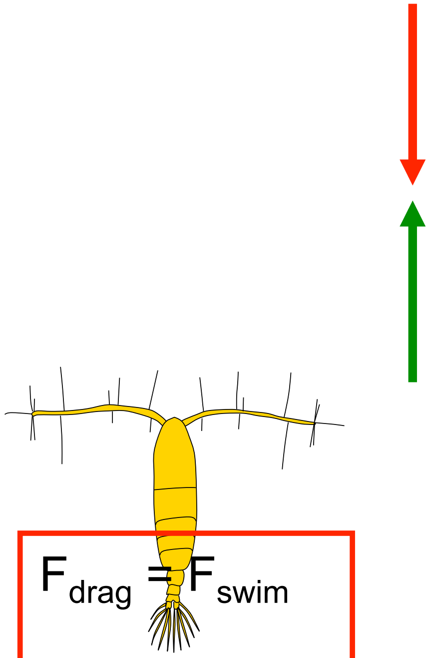
$F_{\text{feeding current}}$

F_{tether}

$F_{\text{tether}} = F_{\text{feeding current}}$

STOKESLET

Cruising copepod



F_{drag}

F_{swim}

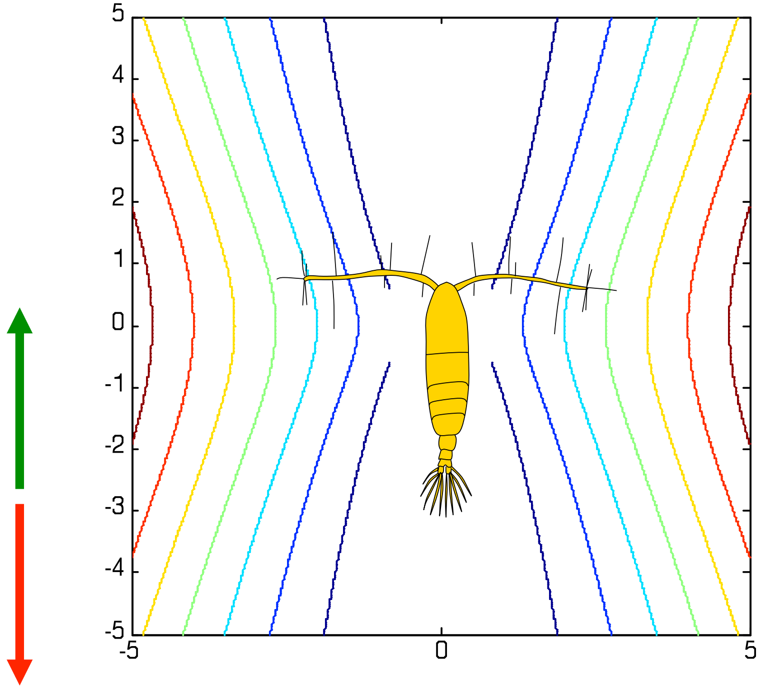
$F_{\text{drag}} = F_{\text{swim}}$

DIPOLE

Kiørboe 2010 Biol Rev

Hovering or cruising?

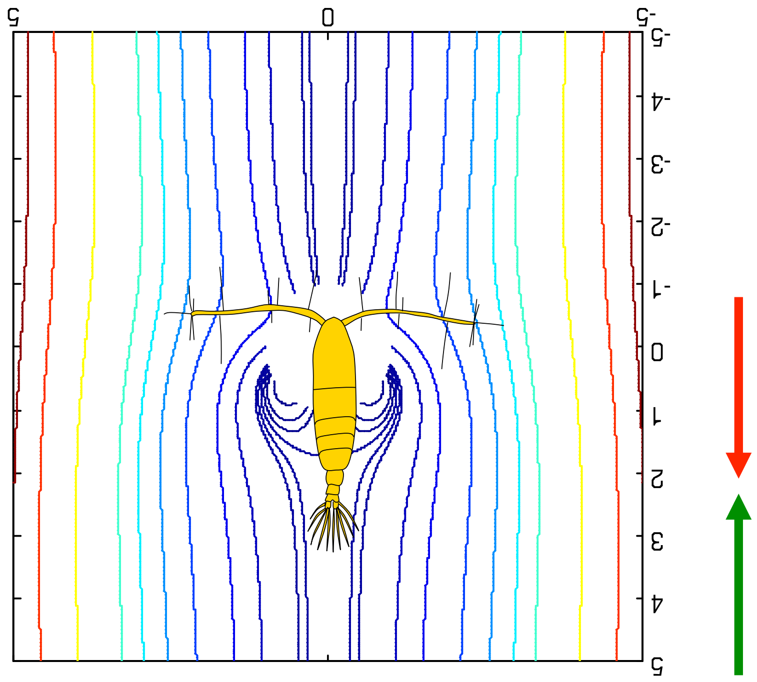
Tethered copepod



$F_{gravity} = F_{swim}$

STOKESLET

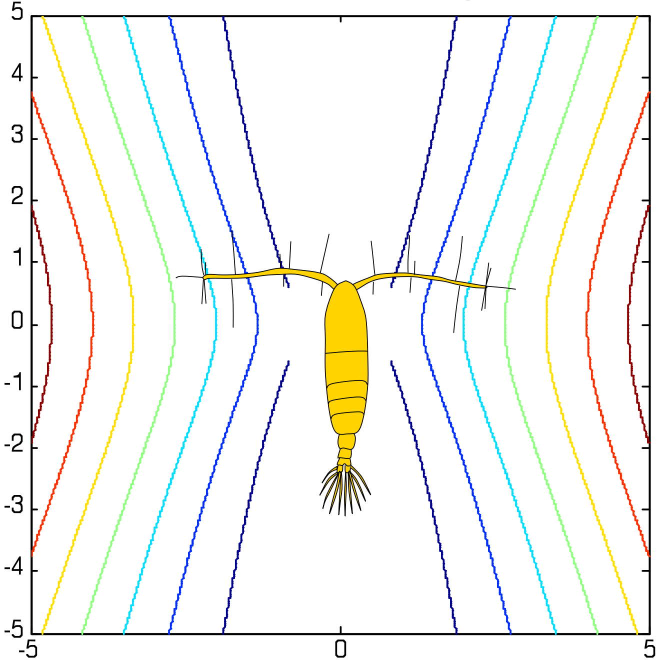
Cruising copepod

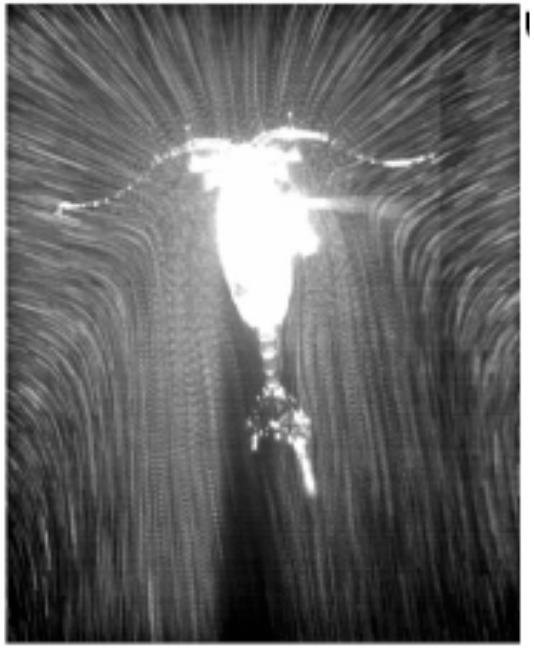


$F_{drag} = F_{swim}$

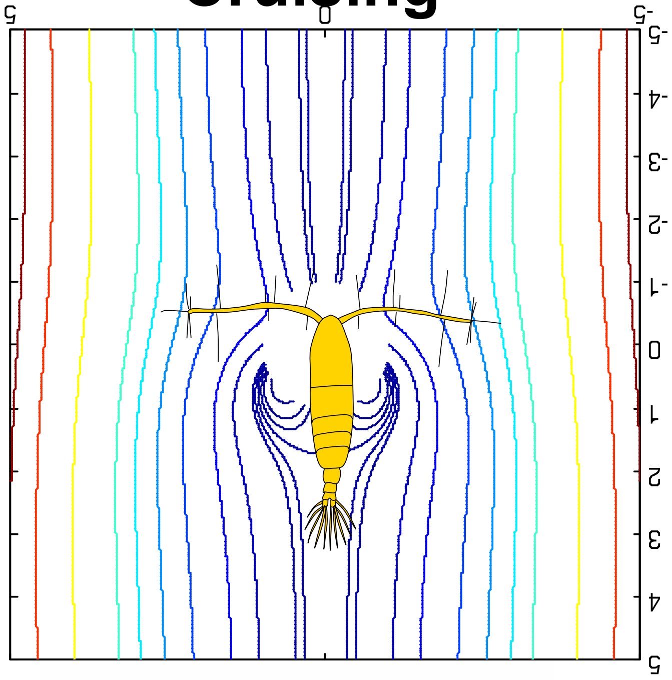
DIPOLE

Hovering





Cruising



Catton et al.
JEB 2007

4 solutions

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- **Cruise feeding**
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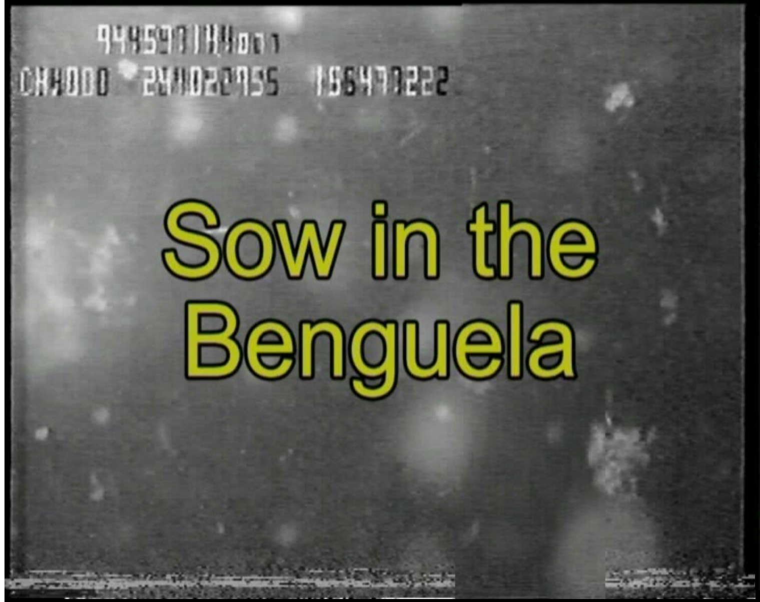
  - **Hunting large particles**

Marine snow

In situ video

↓

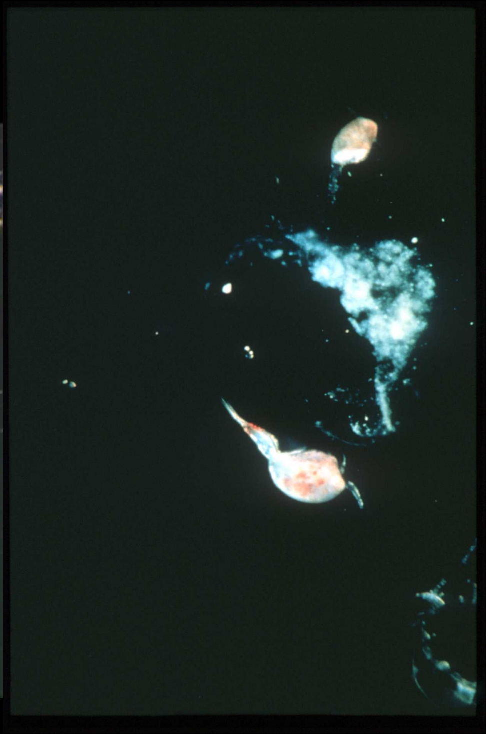


50 µm

Kiørboe et al. LO 1998

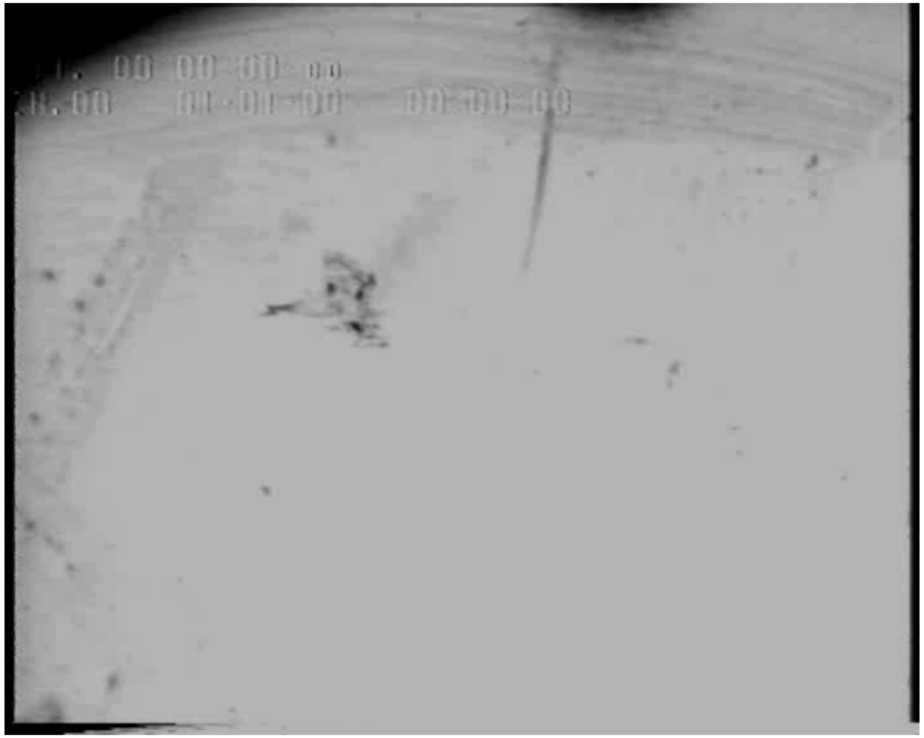
200 µm

Kiørboe JPR 2007



Alice Alldredge photo

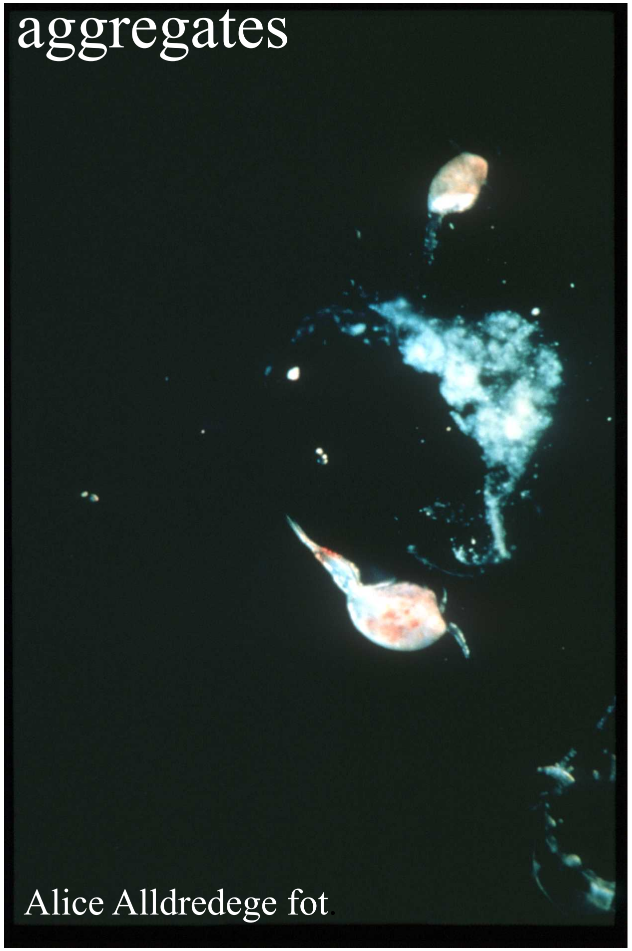
Zooplankters feed on the surface of aggregates



Microsetella norvegica feeding on Aggregate

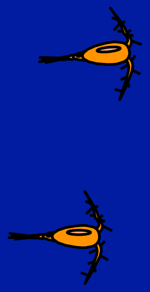
Video: Marja Koski

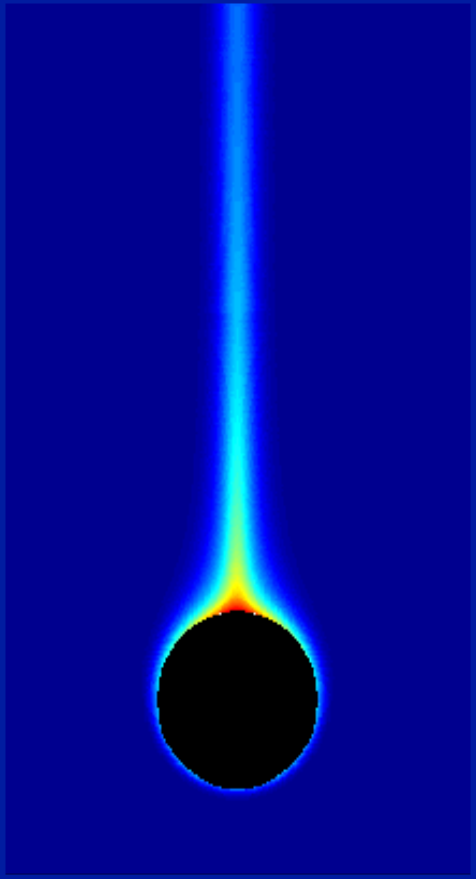
Oncaea sp. Feeding on aggregates



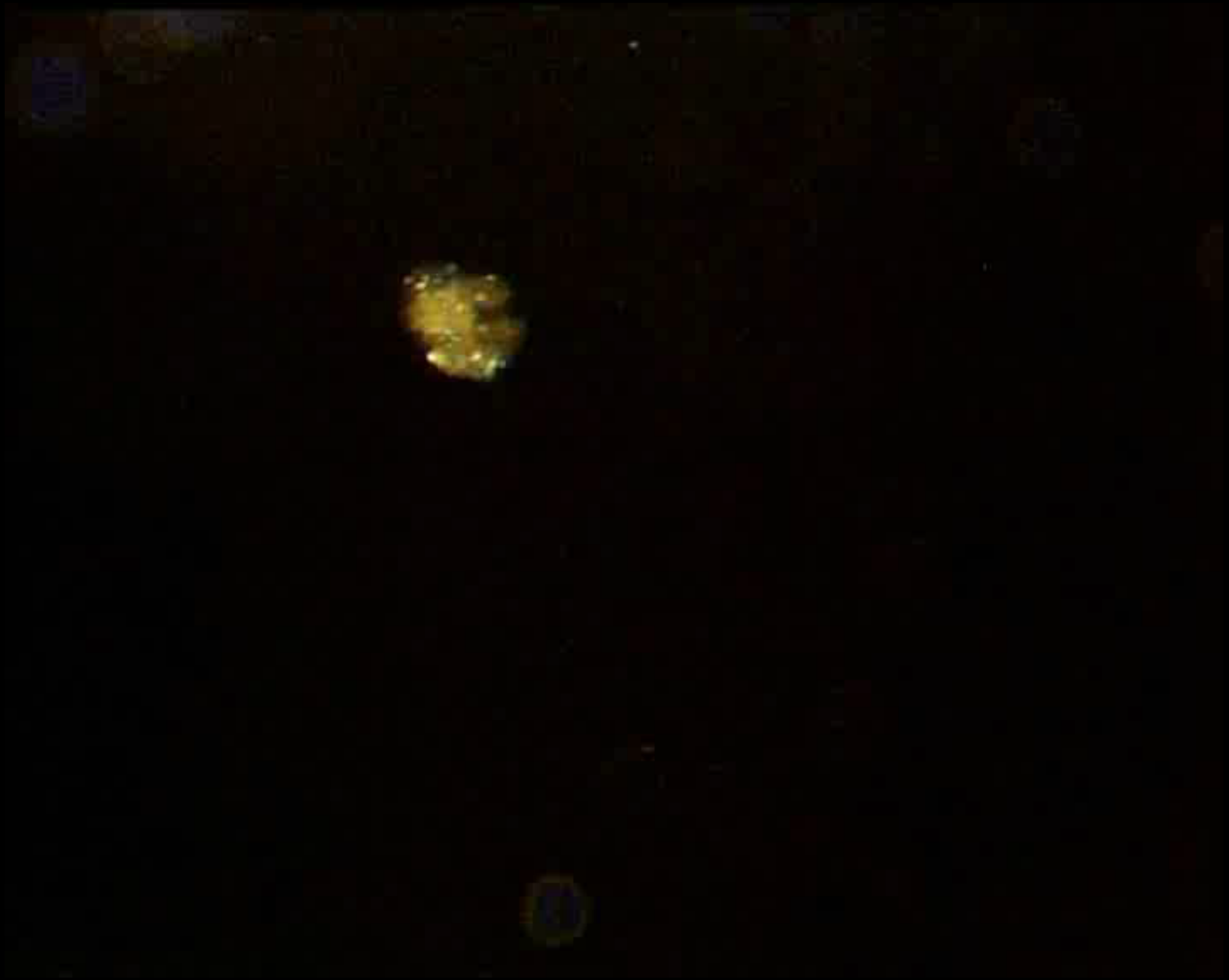
Alice Alldredege fot

How to find an aggregate?





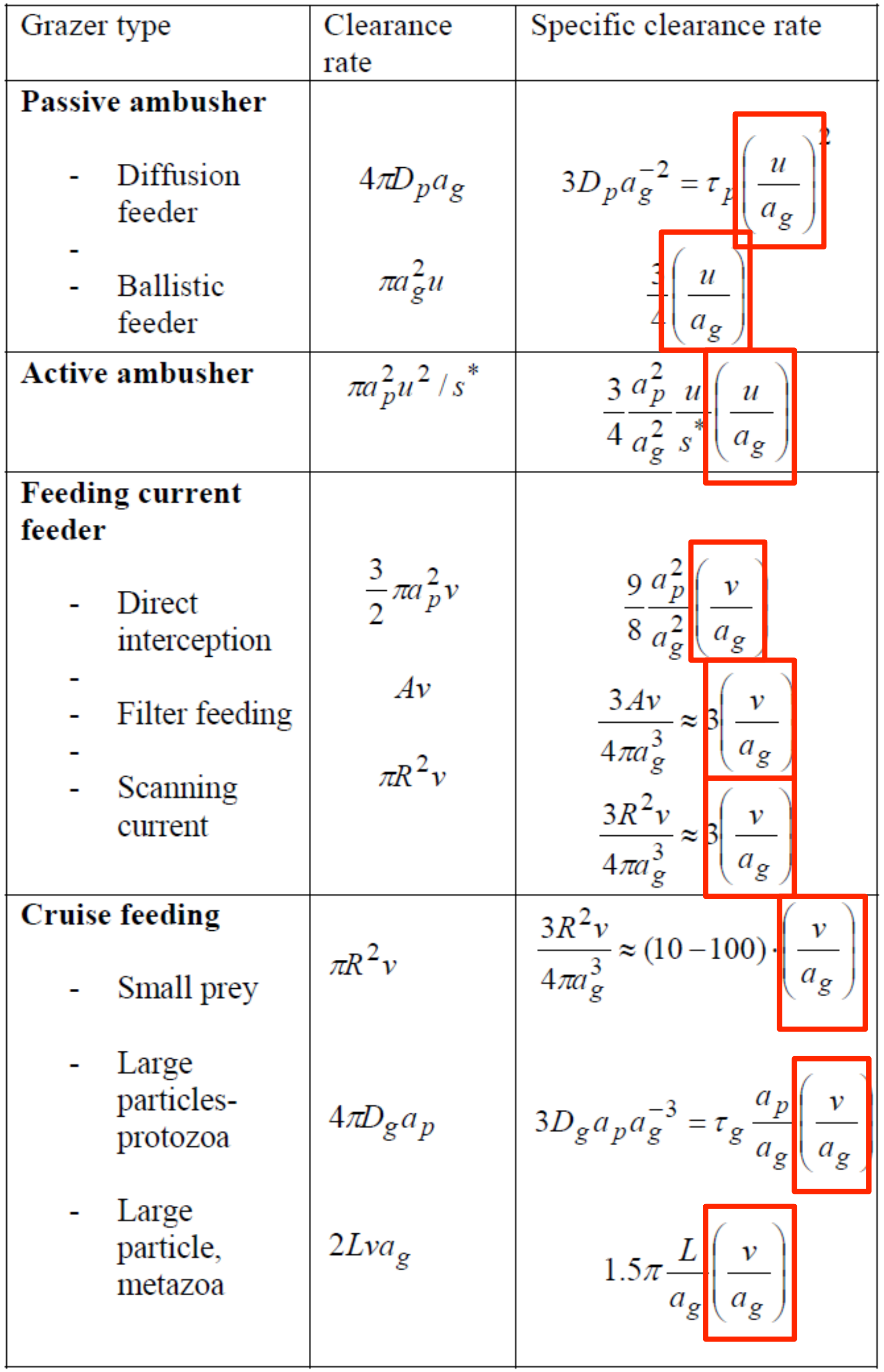
An edible aggregate



Lombard & Kiørboe in prep

SUMMING UP

specific clearance of all feeding mechanisms scale with **velocity/size**



Grazer type	Clearance rate	Specific clearance rate
Passive ambusher		
- Diffusion feeder	$4\pi D_p a_g$	$3D_p a_g^{-2} = \tau_p \boxed{\left(\frac{u}{a_g}\right)}^2$
- Ballistic feeder	$\pi a_g^2 u$	$\frac{3}{4}\boxed{\left(\frac{u}{a_g}\right)}$
Active ambusher	$\pi a_p^2 u^2 / s^*$	$\frac{3}{4}\frac{a_p^2}{a_g^2}\frac{u}{s^*}\boxed{\left(\frac{u}{a_g}\right)}$
Feeding current feeder		
- Direct interception	$\frac{3}{2}\pi a_p^2 v$	$\frac{9}{8}\frac{a_p^2}{a_g^2}\boxed{\left(\frac{v}{a_g}\right)}$
- Filter feeding	Av	$\frac{3Av}{4\pi a_g^3} \approx 3\boxed{\left(\frac{v}{a_g}\right)}$
- Scanning current	$\pi R^2 v$	$\frac{3R^2 v}{4\pi a_g^3} \approx 3\boxed{\left(\frac{v}{a_g}\right)}$
Cruise feeding		
- Small prey	$\pi R^2 v$	$\frac{3R^2 v}{4\pi a_g^3} \approx (10-100)\cdot\boxed{\left(\frac{v}{a_g}\right)}$
- Large particles-protozoa	$4\pi D_g a_p$	$3D_g a_p a_g^{-3} = \tau_g \frac{a_p}{a_g}\boxed{\left(\frac{v}{a_g}\right)}$
- Large particle, metazoa	$2Lva_g$	$1.5\pi\frac{L}{a_g}\boxed{\left(\frac{v}{a_g}\right)}$

3 PRINCIPAL FEEDING MODES
Differences in feeding efficiency

AMBUSH < CRUISE < HOVERING

CRUISE < HOVERING

AMBUSH < (HOVERING & CRUISING)

Why are not all zooplankters hovering??

3 PRINCIPAL FEEDING MODES
Differences in feeding efficiency

AMBUSH < CRUISE < HOVERING

AMBUSH < (HOVERING & CRUISING)

Why are not all zooplankters hovering??

$$\boxed{\text{Fitness} = \frac{\text{gain}}{\text{risk}} = \frac{\text{Feeding rate} - \text{Metabolic rate}}{\text{Mortality rate}}}$$

I. THE TRAITS

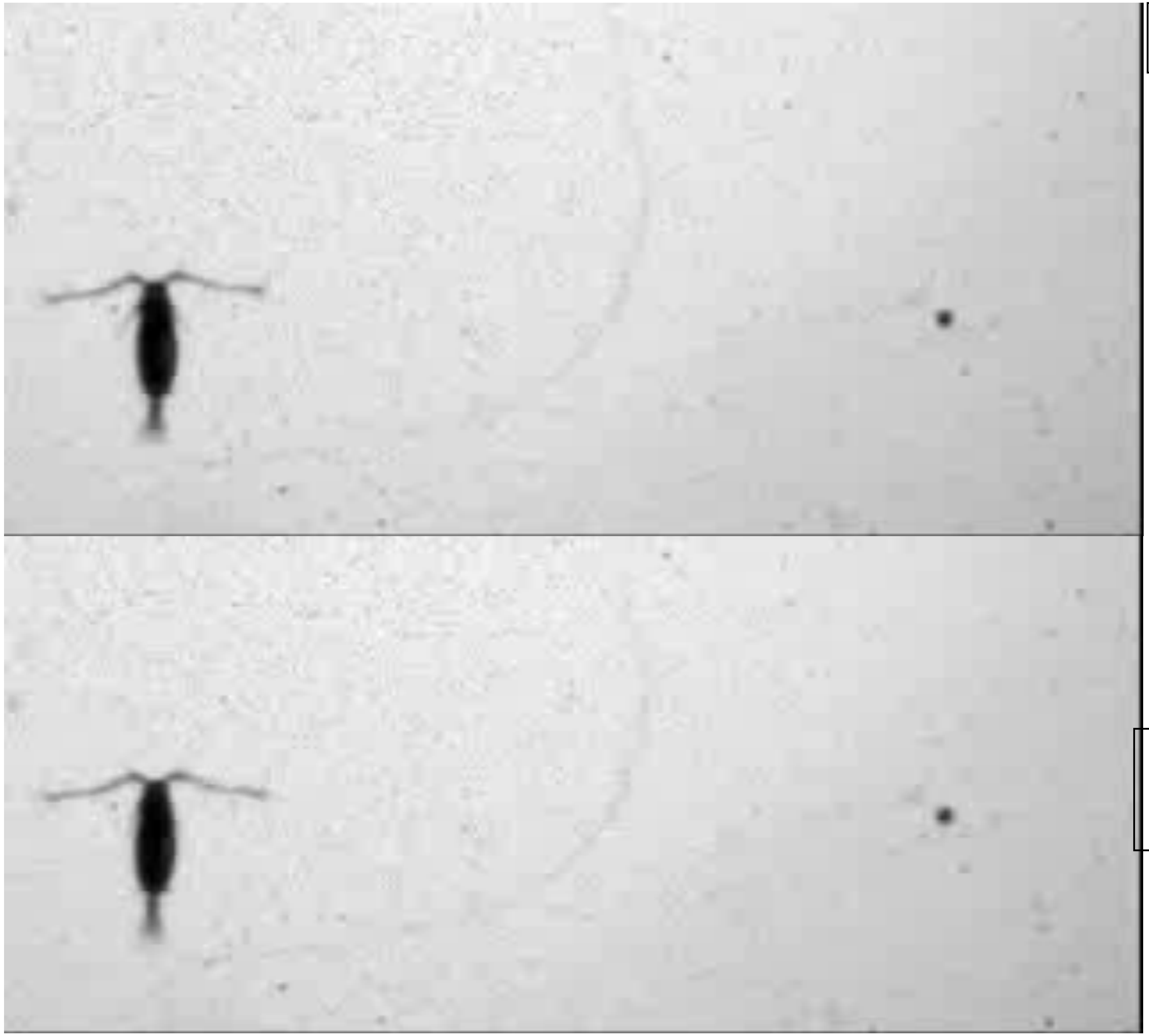
2. Survive

1. Avoid encounters
2. Perceive and escape predators

SURVIVE
Perceive and escape predators

COPEPOD VS FISH

Powerfull escape jump



Real time x 5

Peak velocity:
0.5 m s^{-1}

Peak accelleration:
200 m s^{-2}

Power:
400 watts/kg

Force: 500 N/kg

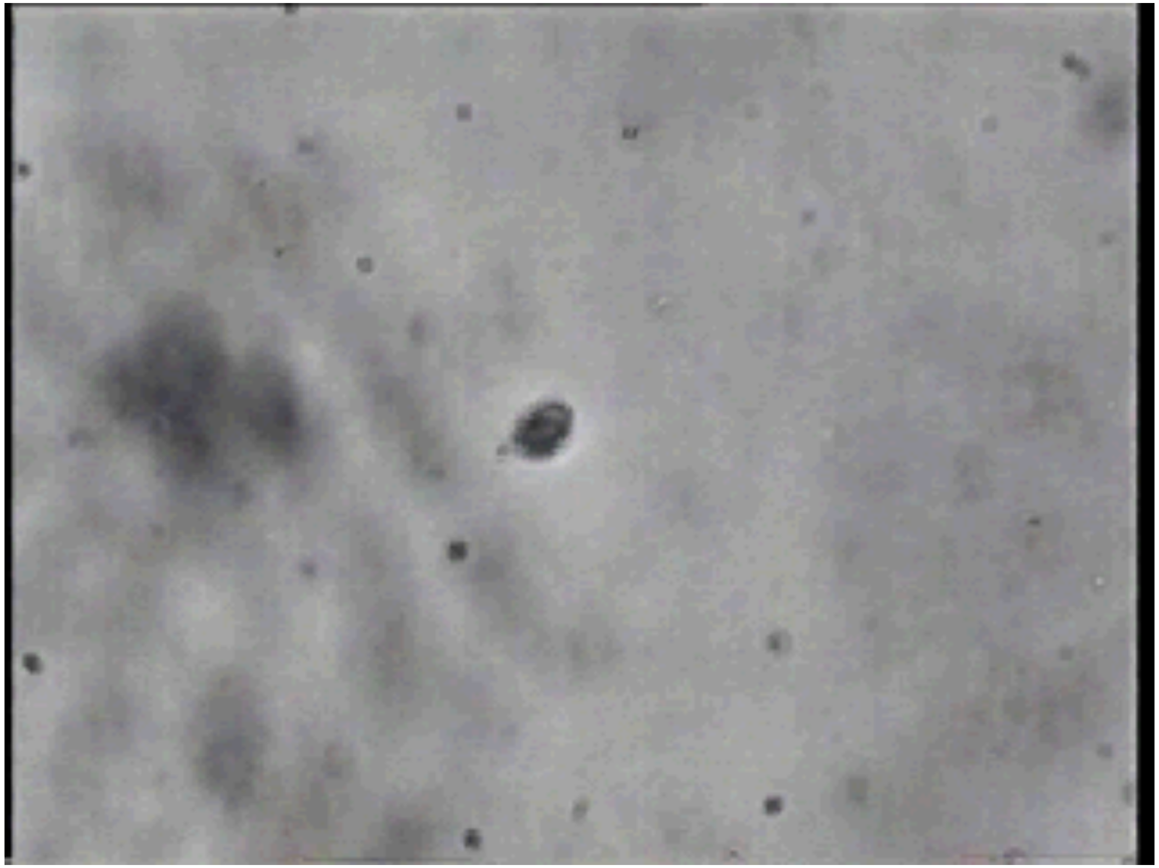
Slow motion
(270 x real time)

1 mm

Kiørboe et al. JRSI 2010

Ciliates entrained in feeding current of *Temora*

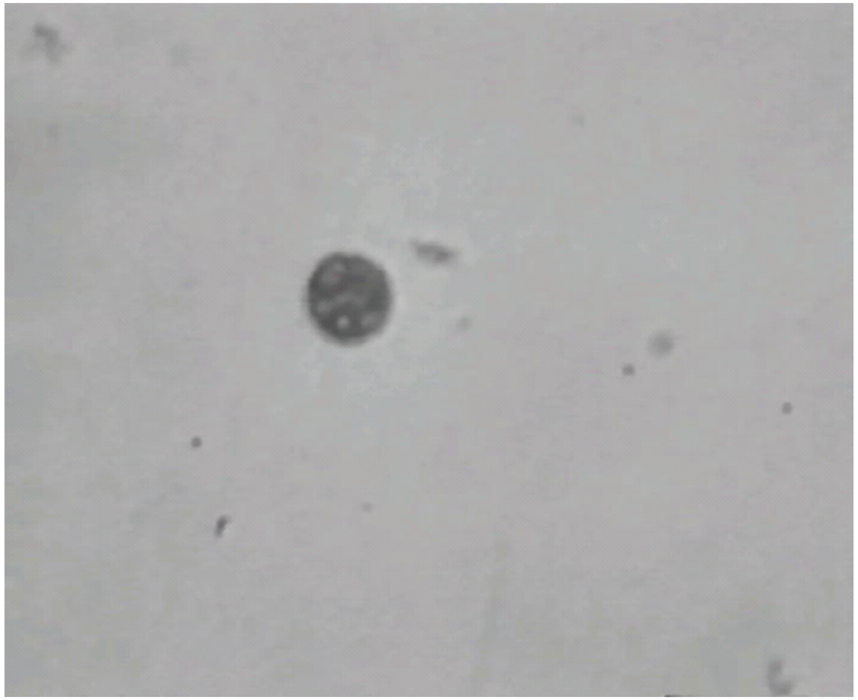
Sesile ciliate feeding on small (3.5 μm) flagellates (*Chrysochromulina*)



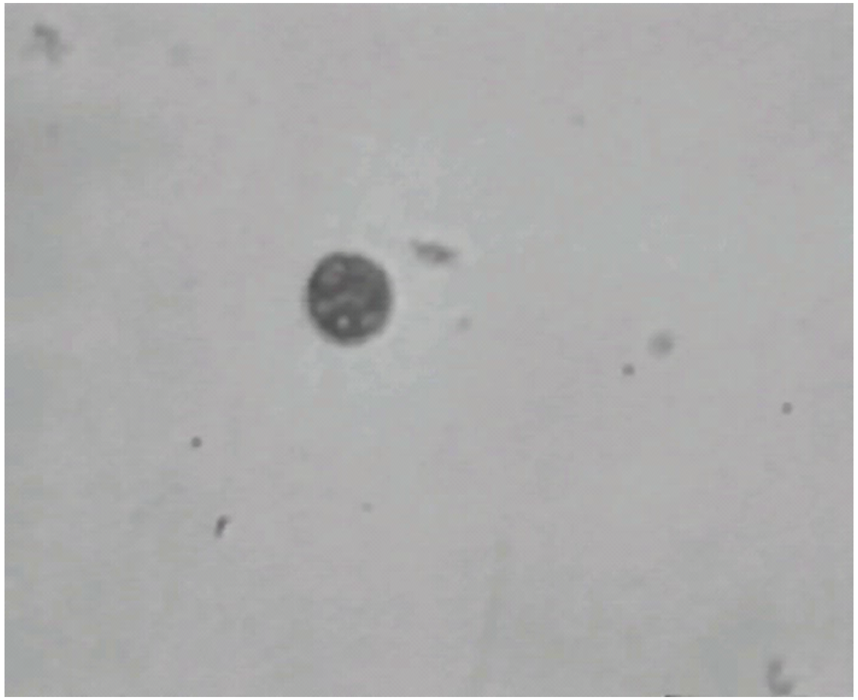
Coutsey of HH Jakobsen

Mesodinium feeding on *Heterocapsa*

Real time



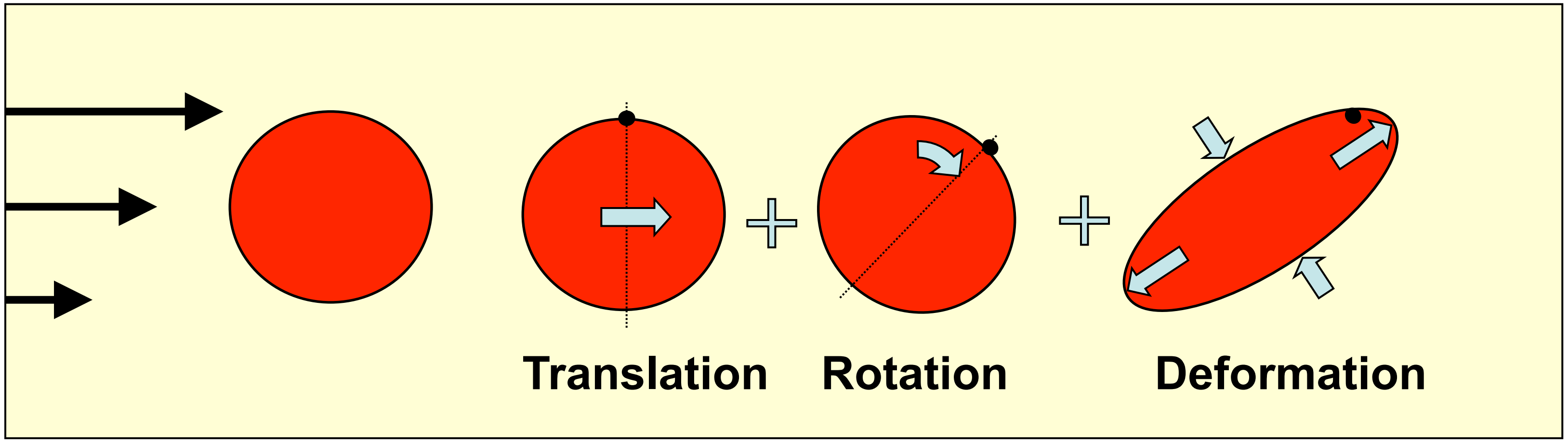
Slo mo



Coutsey of HH Jakobsen

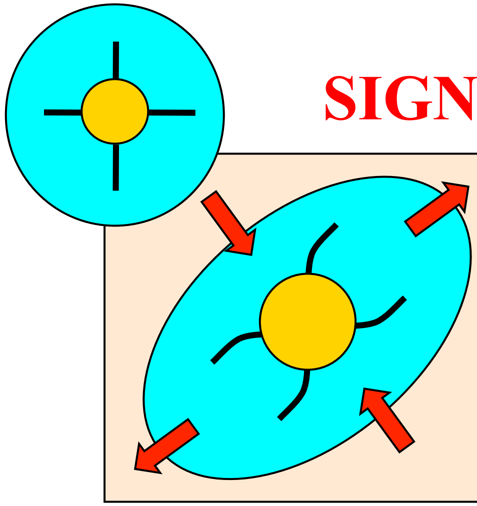
Decomposition of fluid disturbance

In the plankton, perception of individual predators is through the fluid disturbance that the predator generates as it moves



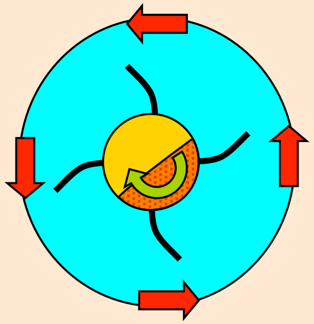
Kiørboe & Visser MEPS 1999

SIGNAL STRENGTH



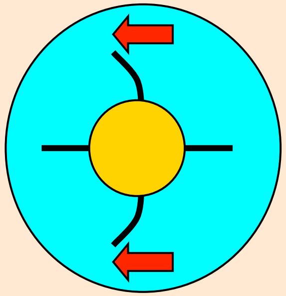
Deformation rate

$S_{\Delta} = L \times \Delta$



Vorticity

$S_{\omega} = \frac{1}{2} L \times \omega$

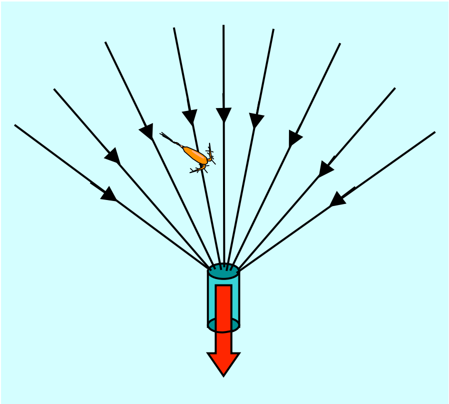


Acceleration

S_a = ‘slip velocity’
$= |a| L^2 (\rho_1 - \rho_2)$

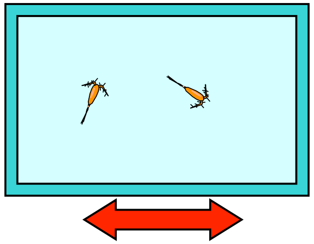
Kiørboe & Visser MEPS 1999

Schematic of experimental setup



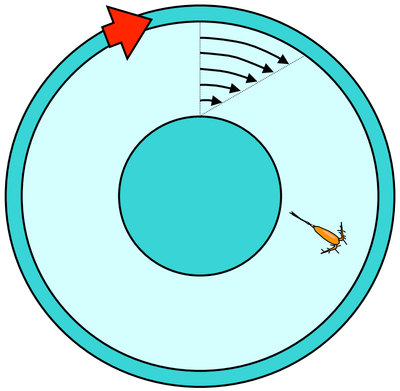
Siphon flow

- longitudinal deformation
- acceleration



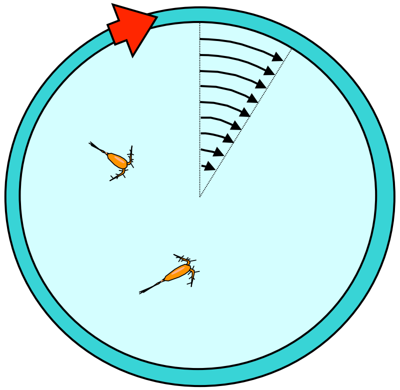
Oscillating chamber

- acceleration



Couette device

- shear deformation
- acceleration
- vorticity

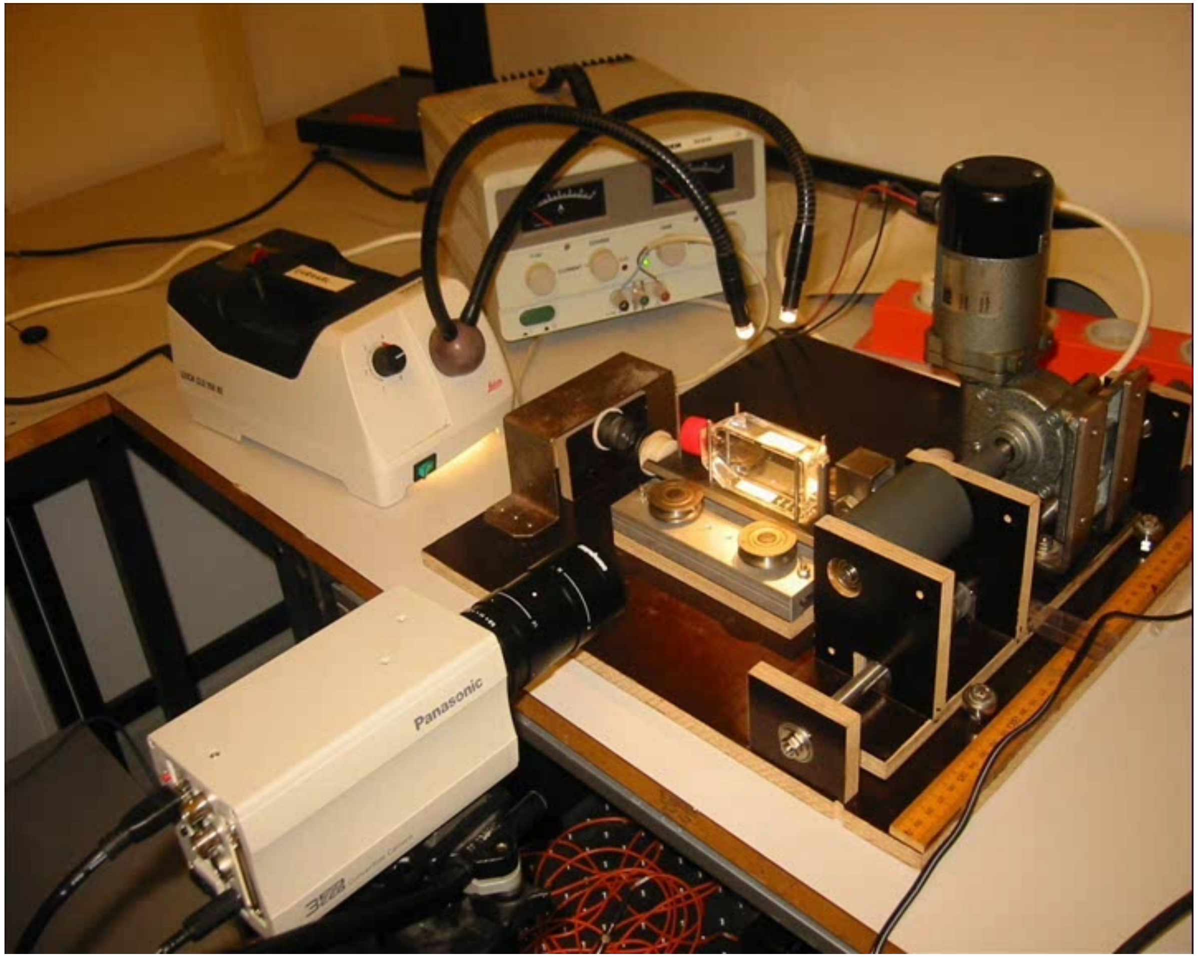


Rotating cylinder

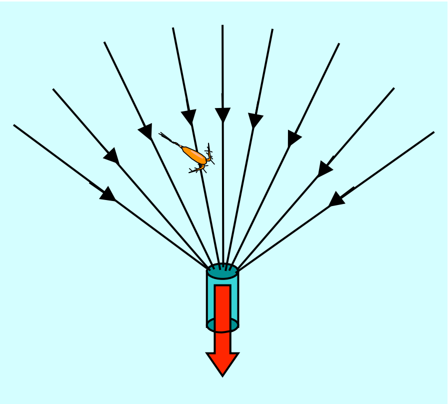
- acceleration
- vorticity

Kiørboe et al. MEPS 1999

Demo of oscillating chamber

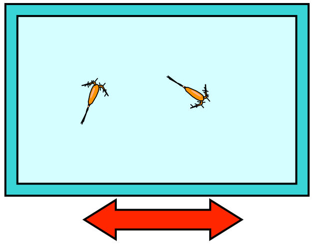


Schematic of experimental setup



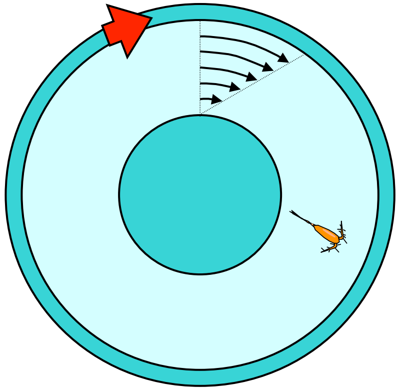
Siphon flow

- longitudinal deformation
- acceleration



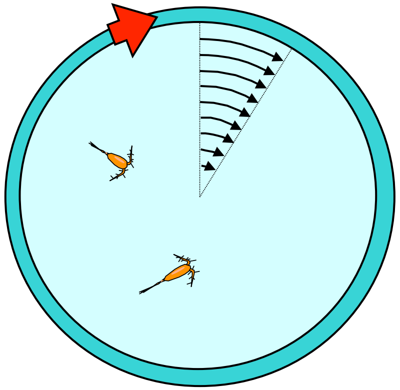
Oscillating chamber

- acceleration



Couette device

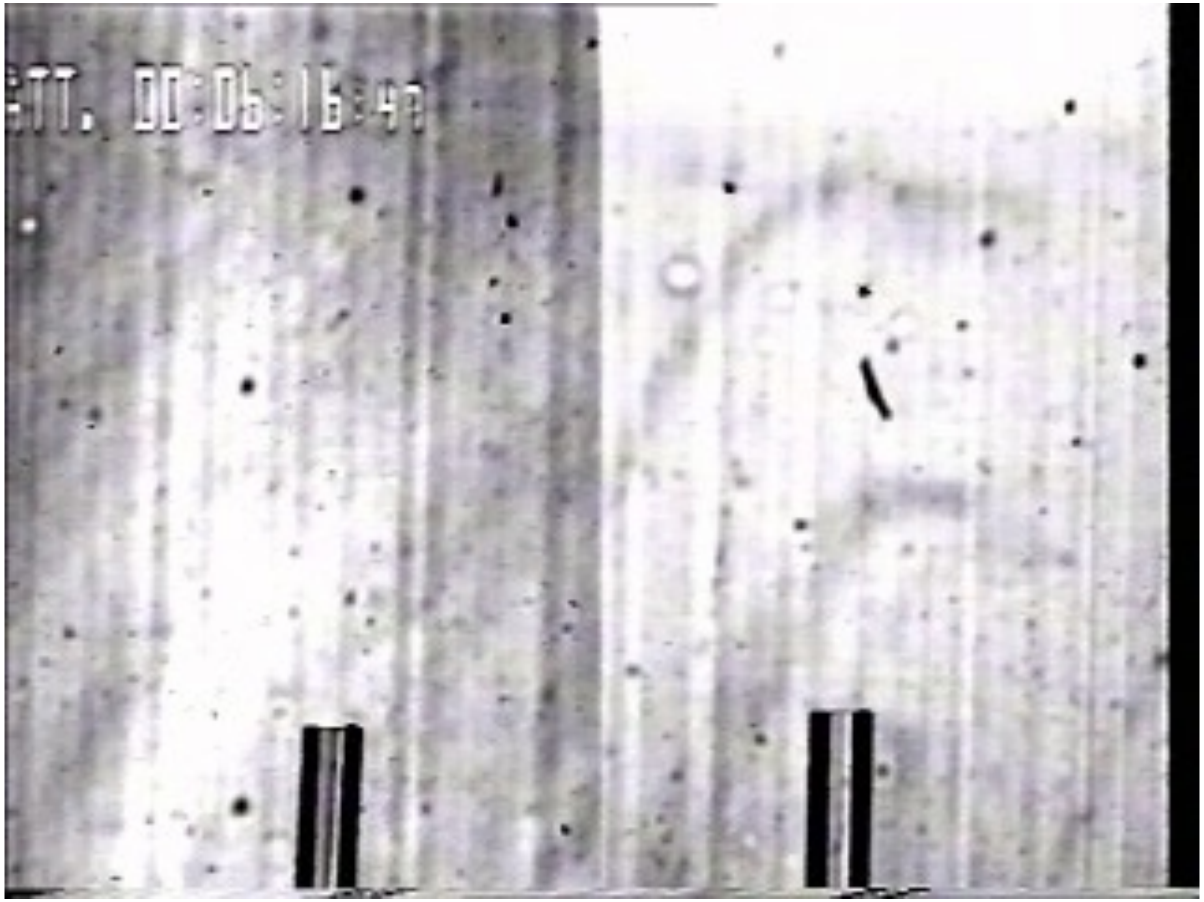
- shear deformation
- acceleration
- vorticity



Rotating cylinder

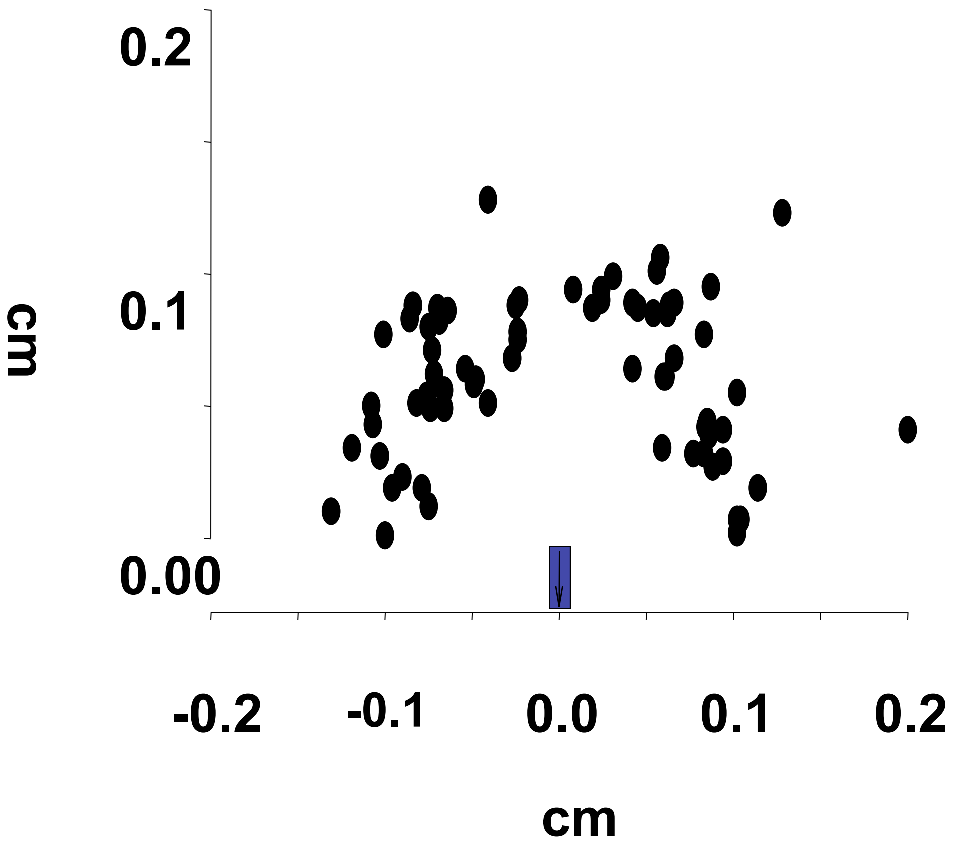
- acceleration
- vorticity

Pipette experiment: *Calanus* nauplii



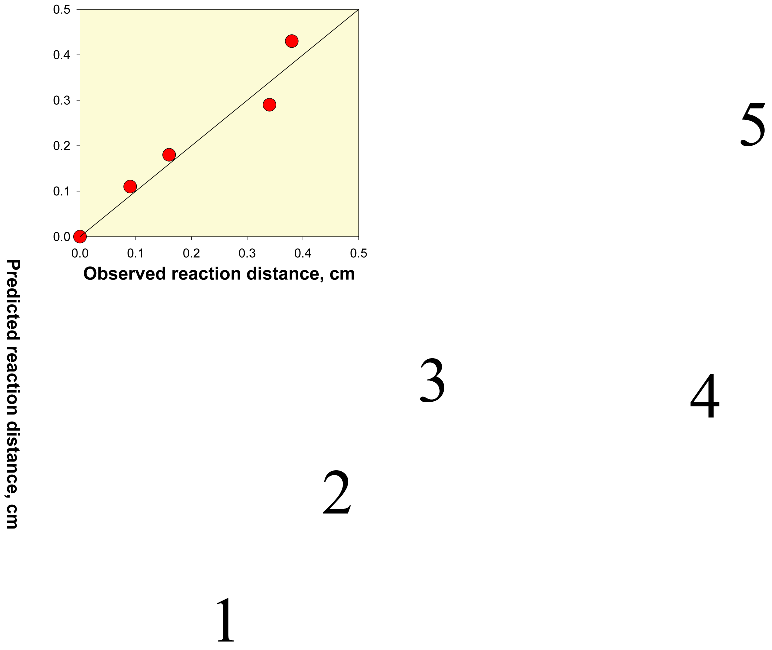
Kiørboe et al. MEPS 1999

Spatial distribution of escape jumps in siphon flow *Balanion comatum* (ciliate)



HH Jacobsen

Observed and predicted reaction distances



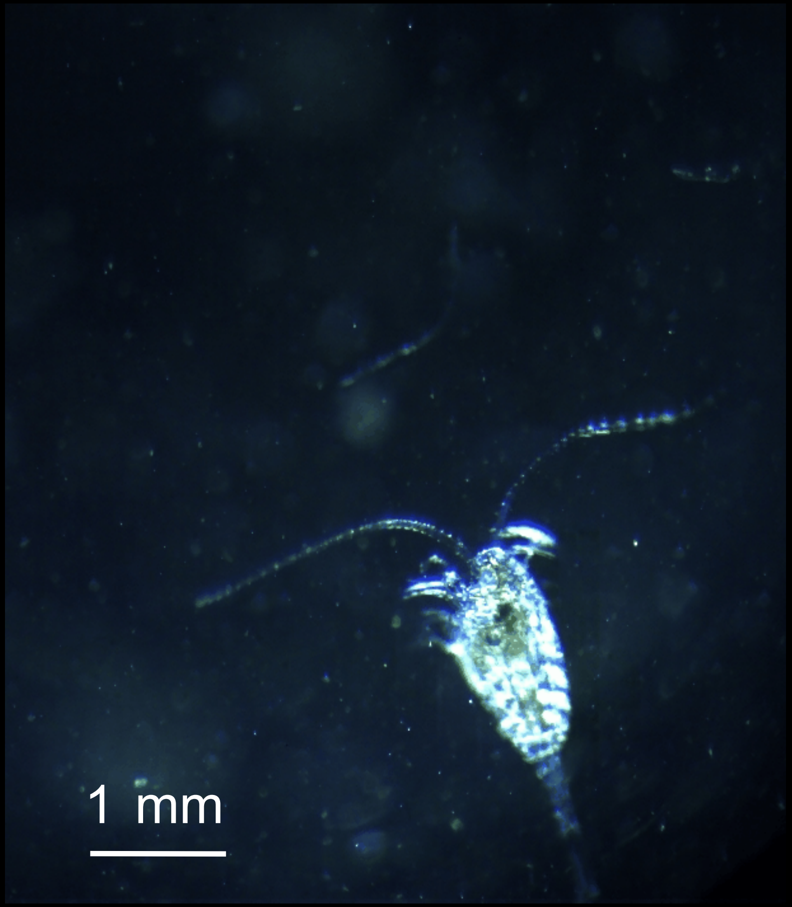
1: Stickleback-*Temora*; 2: *Centropages*-*Acartia* nauplii;
3: *Temora*-*Acartia* nauplii; 4: Stickleback-*Eurytemora*;
5: Larval cod - *Acartia* nauplii

Kiørboe 2008

Swimming modes

’Smooth’ swimming

(vibration of feeding appendages)



SloMo: 140x

Erratic swimming

(jumps with swimming legs)

0.2 mm

Swimming modes

’Smooth’ swimming

(vibration of feeding appendages)

2 mm

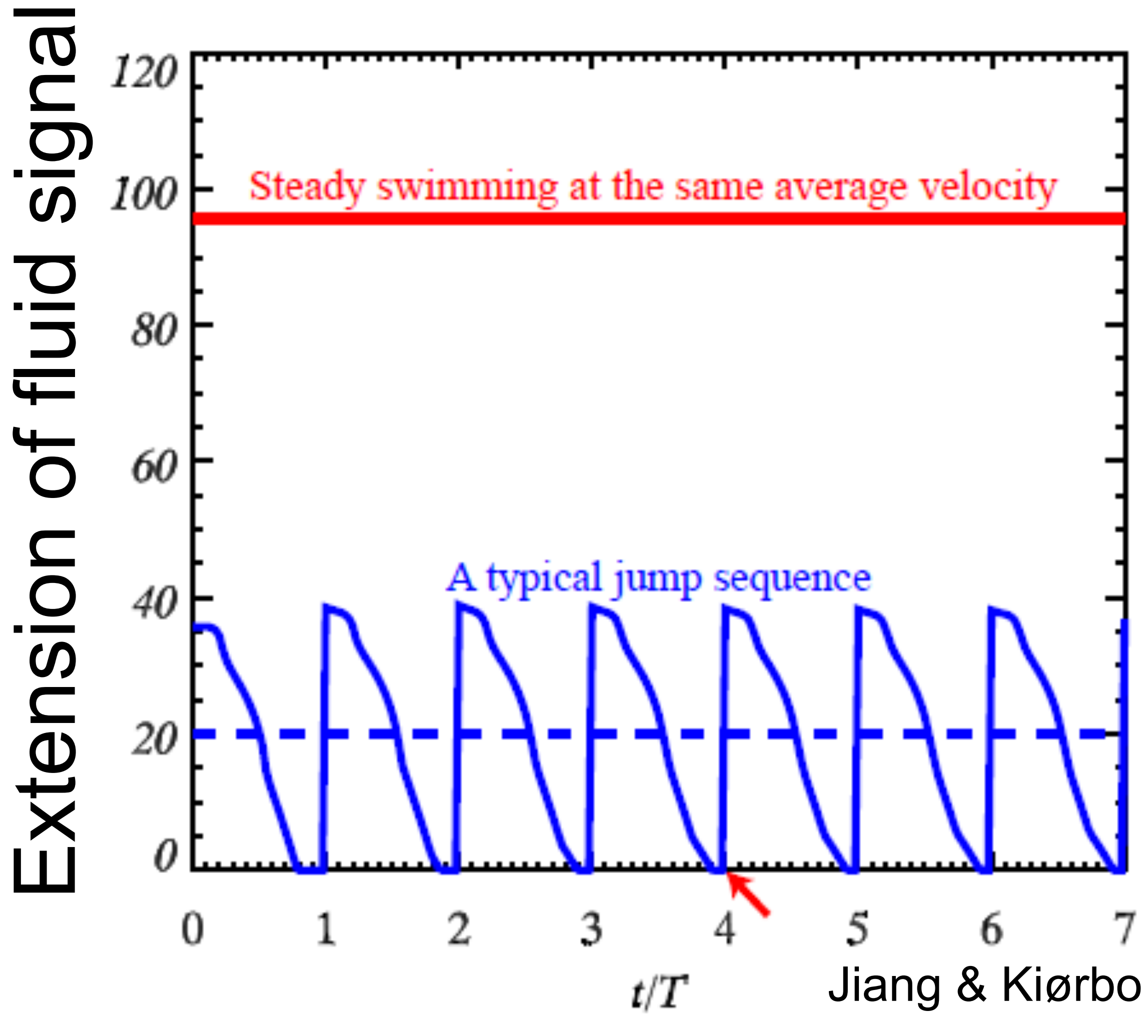
Erratic swimming

(jumps with swimming legs)

0.2 mm

Both are in SloMo

Different swimming modes yield different fluid signals



Steady swimming

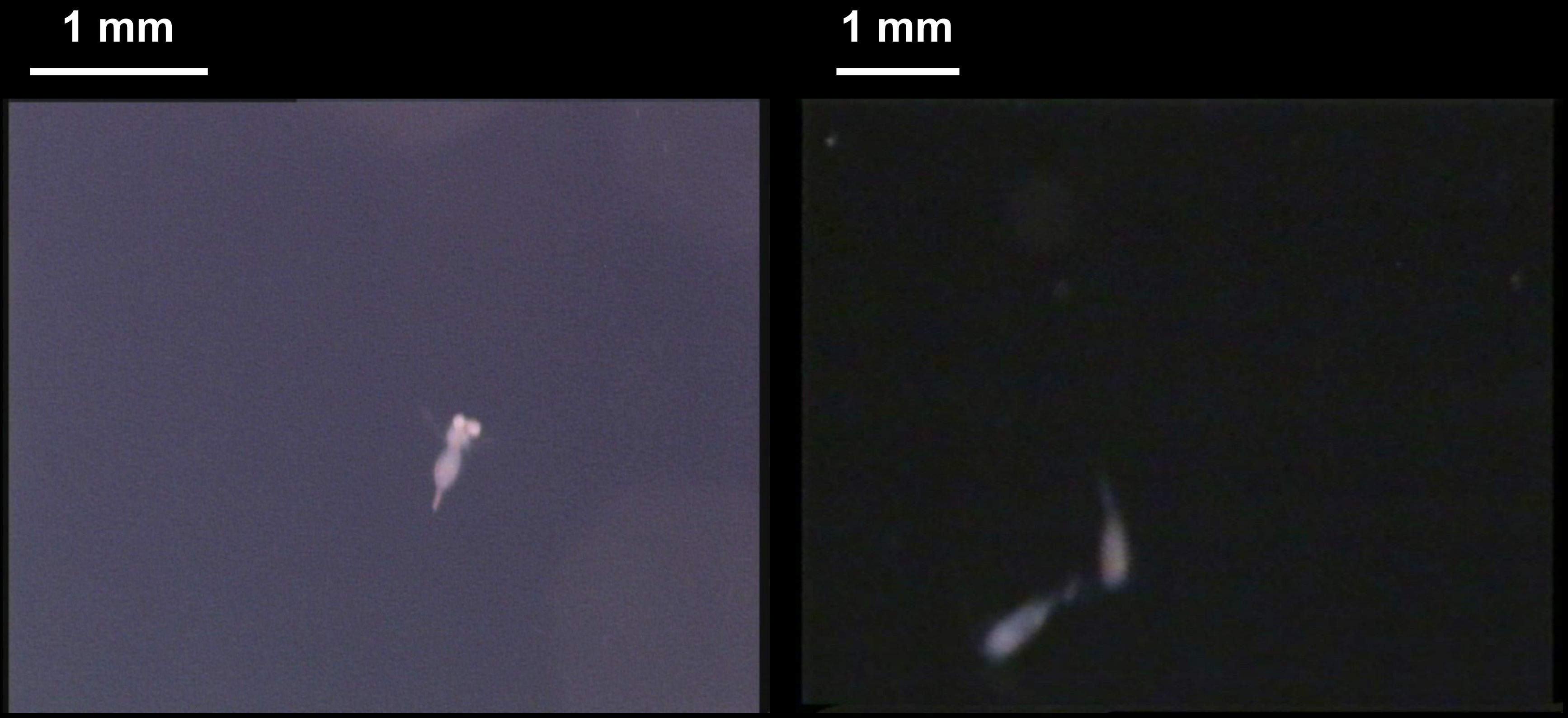
Jump swimming

Jiang & Kiørboe, J R Soc Interface 2010

I. THE TRAITS:

3. Reproduce

REPRODUCTION
The ultimate Darwinian mission



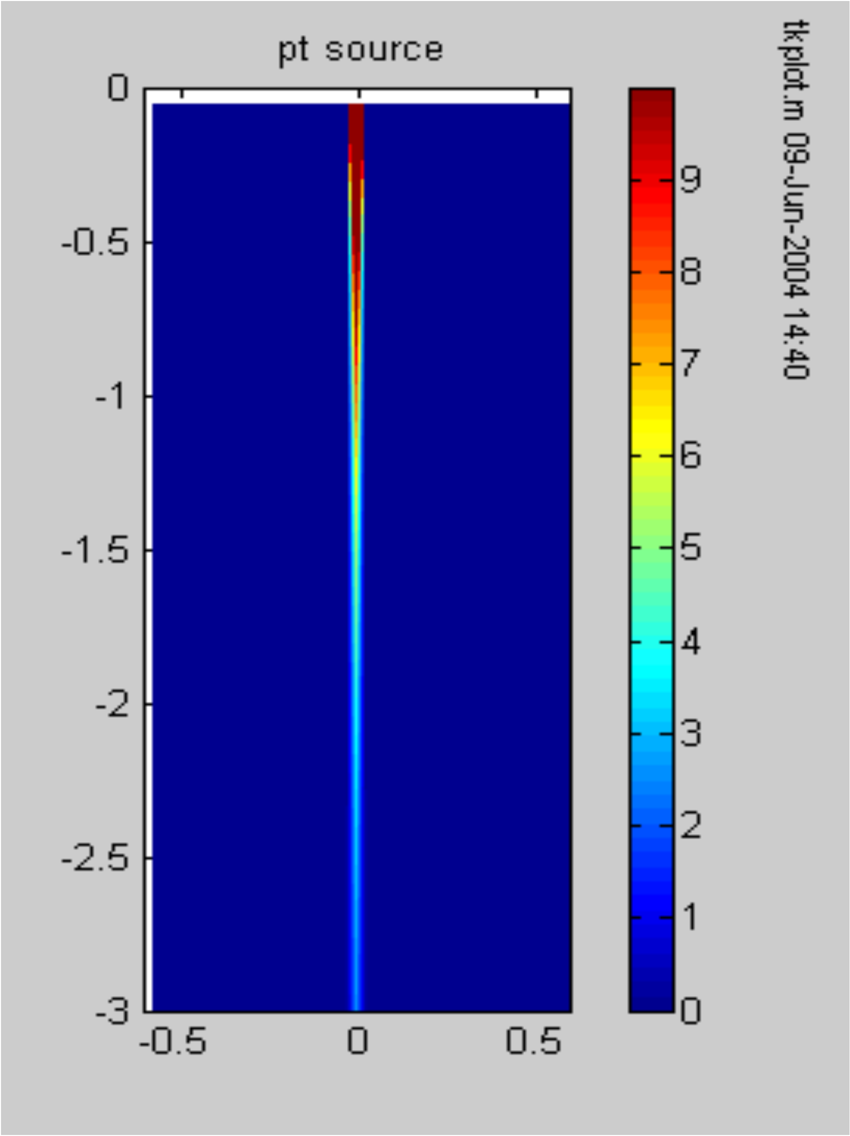
Copepods in private situations

How do mates find one another in a 3-dimensional world

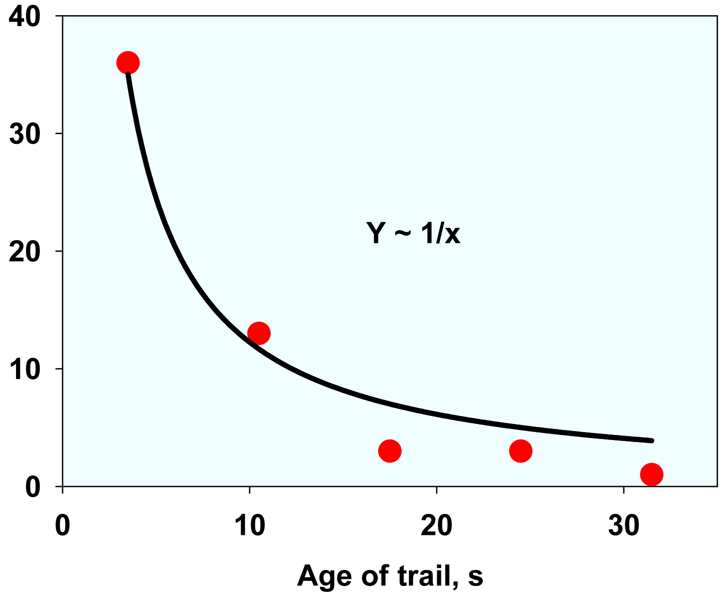
Centropages typicus

Bagøien & Kiørboe MEPS 2005

Moving point source



$$\boxed{\enclose{circle}{C} = \frac{Q}{4\pi D\enclose{circle}{z}}}\cancel{\exp\left(-\frac{ur^2}{4Dz}\right)}$$



Bagøien & Kiørboe MEPS 2005

Oithona davisae
An ambush feeder

Oithona: male finds female

Mirror in diagonal of aquarium to get 3-D

Kiørboe LO 2007

Oithona: Male finds females

Female

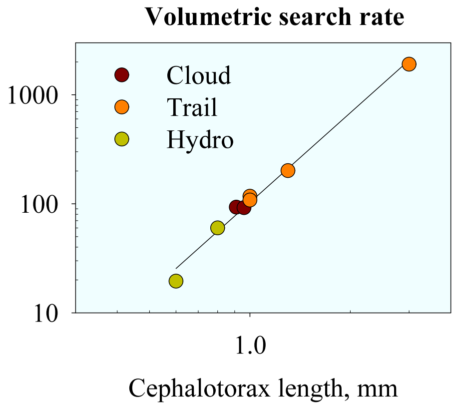
Her mirror image

Kiørboe LO 2007

Acartia: Hydrodynamic signal

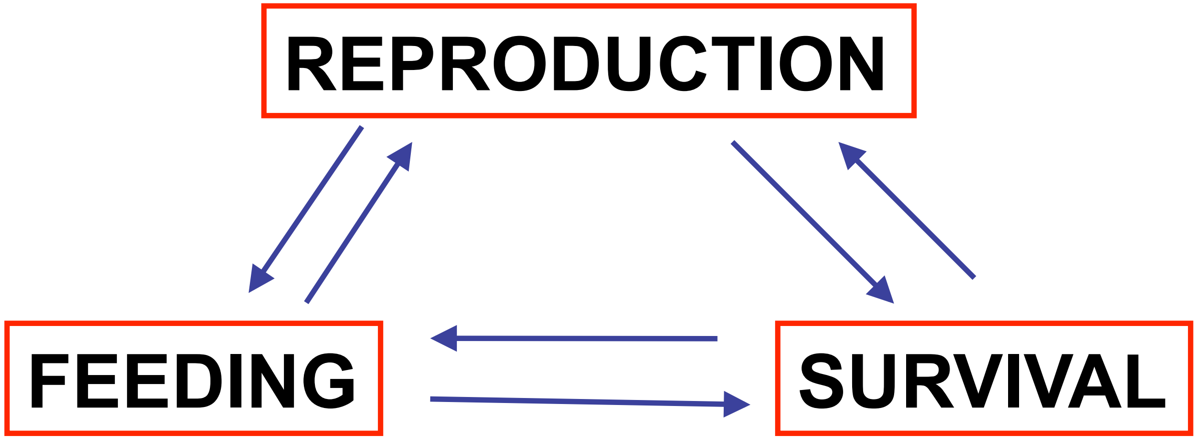
Bagøien & Kiørboe MEPS 2005

VOLUMETRIC SEARCH RATE
Mating is rarely encounter limted



Kiørboe & Bagøien LO 2005

II. TRADE OFFS
Conflicts between fundamental activities



REPRODUCTION

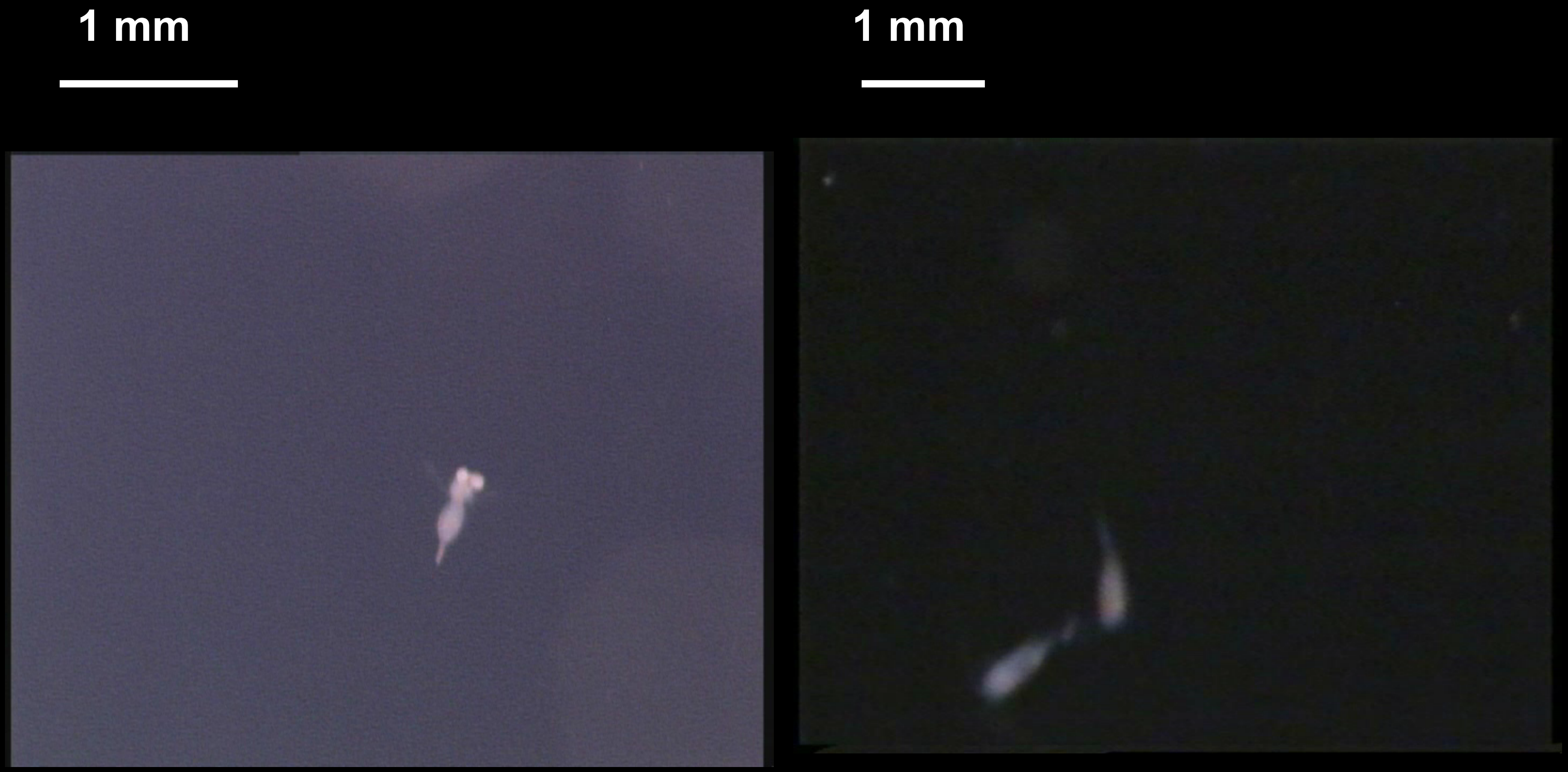
FEEDING

SURVIVAL

Two examples (Fitnes optimization):

- *Feeding behavior, mate finding and predation risk*
- *Feeding behavior, fluid signal and predation risk*

How will a non-motile ambush feeder ever meet a mate?



Copepods in private situations

Ambush feeders: The males have to sacrifice feeding

Males on a mission

How much and how fast to swim?

---

swimming implies:

- **Mate encounters**
- **Reduced feeding**
- **More predator encounters**
- **Higher energetic costs**

Male fitness (*G*):

***G*(behavior) = Mate encounter rate/mortality rate = number of life-time mate encounters**

The fitness function

Fitness: $$G(v,p) = \frac{K_1 vp}{K_2(u^2+v^2)^{0.5}}$$

← **Mate encounter rate**

← **Predator encounter rate**

v: male swimming velocity
p: fraction of time swimming
u: predator swimming velocity
K_1, K_2: constants

How much (*p*) and how fast (*v*) to swim?

Assume energy balance

- – Constant basal metabolism (M)
- – Fraction of time spend swimming: p
- – Swimming cost increases with v^2: $a \times v^2 \times p$
- – Food intake: $f \times (1-p)$
- – Energy balance (Input = output):

$$\boxed{M + av^2 p = f(1 - p)}$$

Behavior that optimizes fitnes

Optimize:

$$\frac{dG(v,p)}{dp} = 0$$

$$v = \left(\frac{f(1-p) - M}{\alpha p}\right)^{1/2}$$

$$\boxed{p = \frac{-\left(4fM - 4f^2 + \alpha f u^2 - \alpha M u^2\right) \pm (f - M)u\sqrt{\alpha\left(8f + au^2\right)}}{2\left(2f^2 - 2\alpha f u^2\right)}}$$

Without predators

Fraction of time swimming (p):

Values for
for *Oithona*:

PREDICTED **OBSERVED**

$$p = \frac{f - M}{2f}$$

Prediction:
swimming less $\frac{1}{2}$ the time

= 0.36 0.37

Swimming speed:

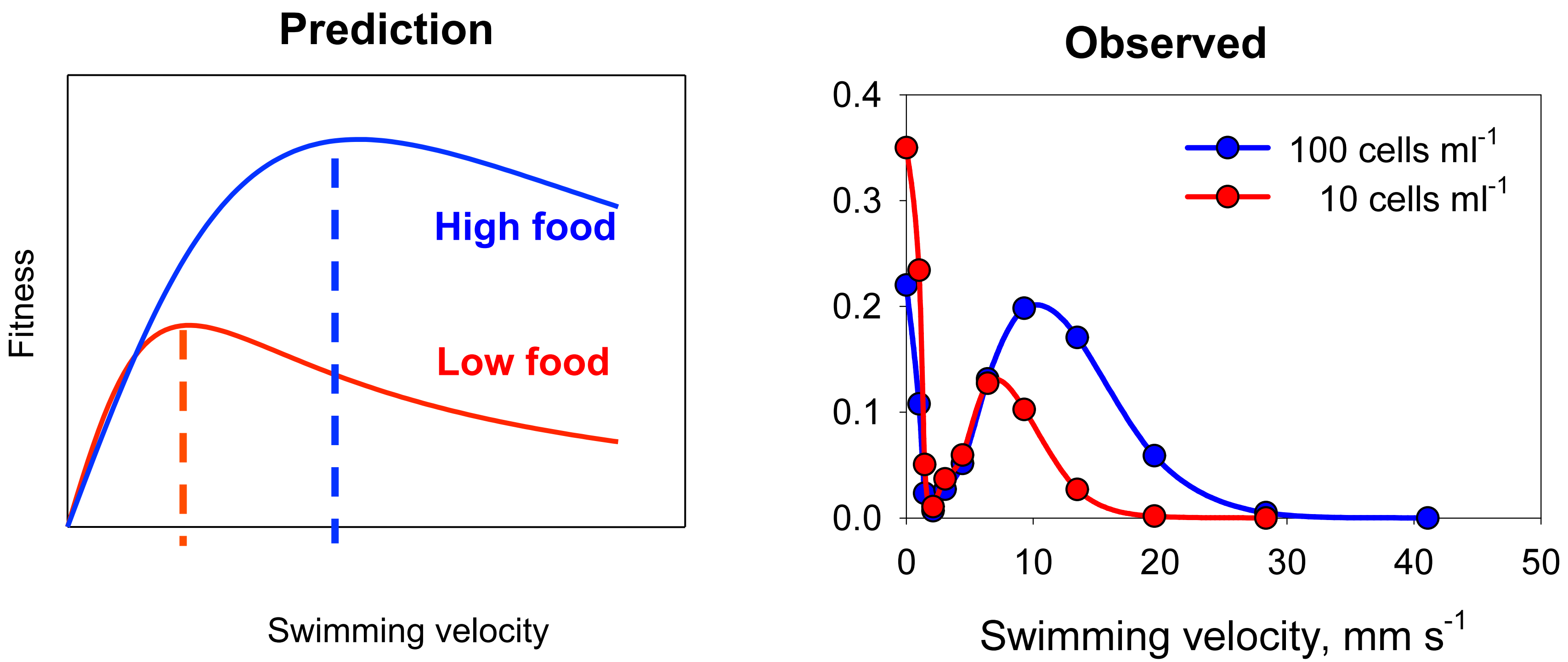
$$v = \left(\frac{f(1-p) - M}{\alpha p} \right)^{1/2}$$

= 14 mm/s 12 mm/s

~ 50 body-length per s
(world copepod record)

Kiørboe Oecologia 2008

Including predation

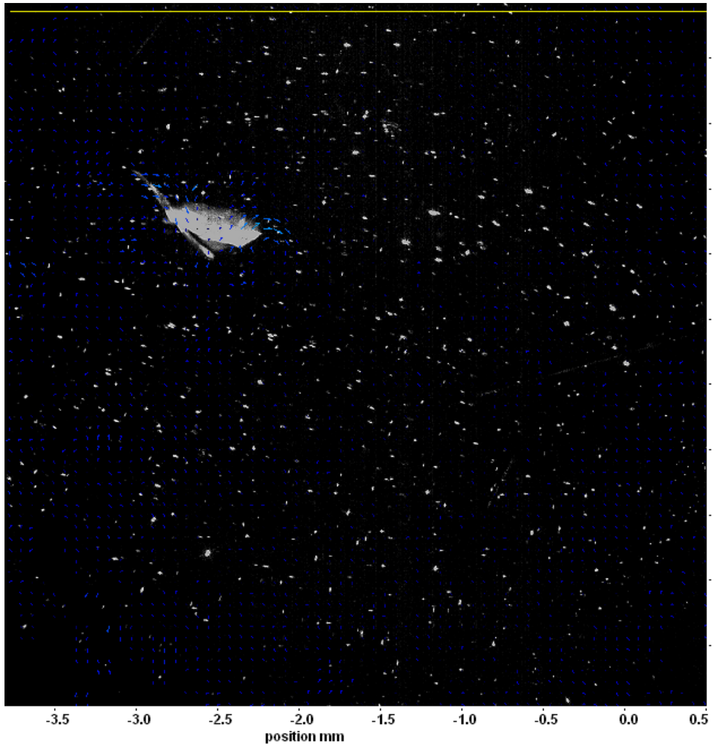


Important point: optimal strategy modulated by the environment

Kiørboe Oecologia 2008

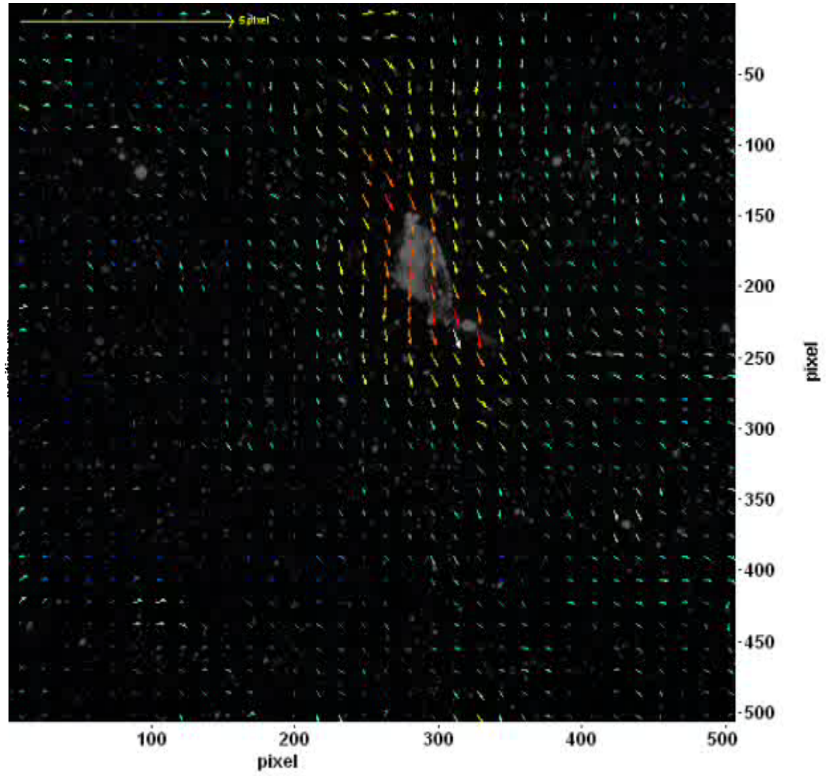
RISK OF FEEDING:
Feeding behavior and fluid signal

Ambush feeding: reposition jump



Rare jumps

Feeding current feeding

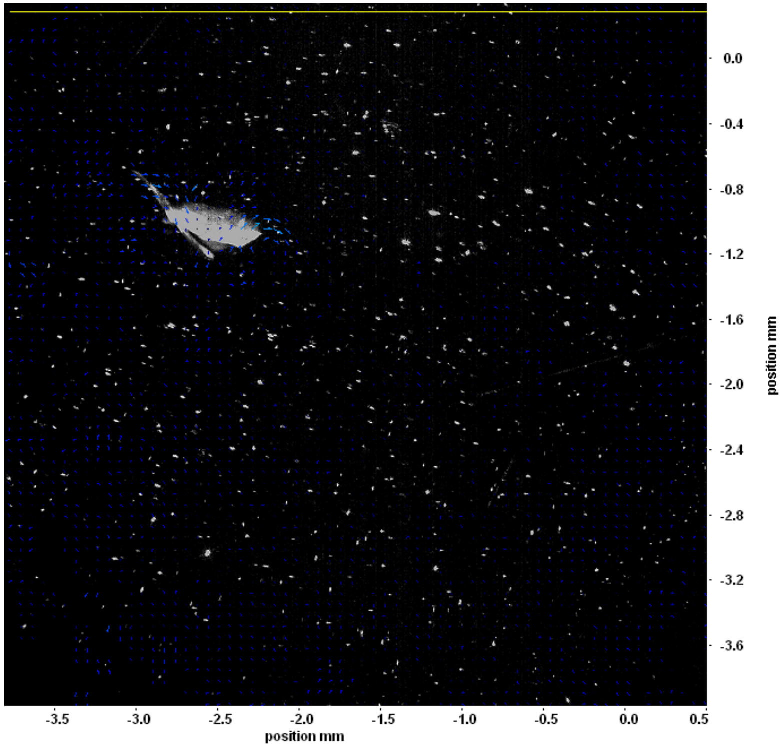


~ Continous feeding current

Kiørboe et al. Proc. Roy Soc B 2010

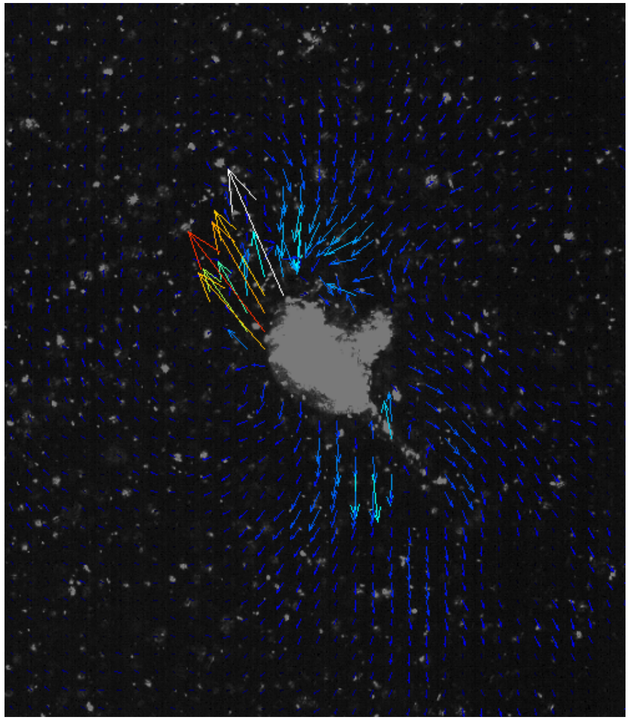
RISK OF FEEDING:
Feeding behavior and fluid signal

Ambush feeding: reposition jump



Rare jumps

Feeding current feeding



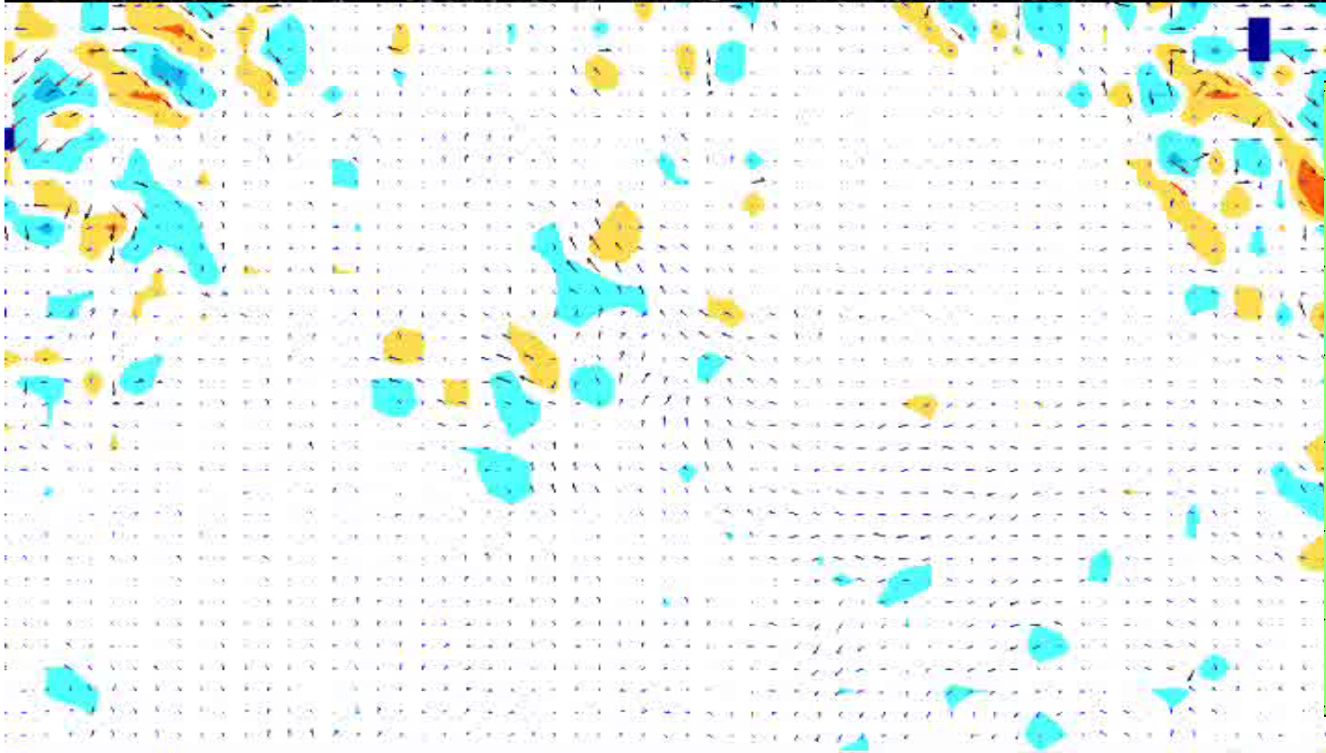
~ Continous feeding current

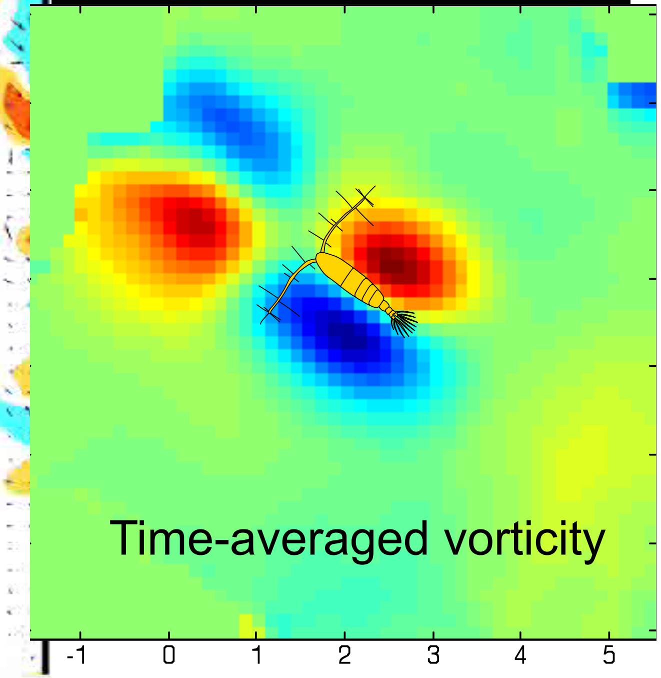
Kiørboe et al. Proc. Roy Soc B 2010

Flow field

Re of reposition jumps: 20-100

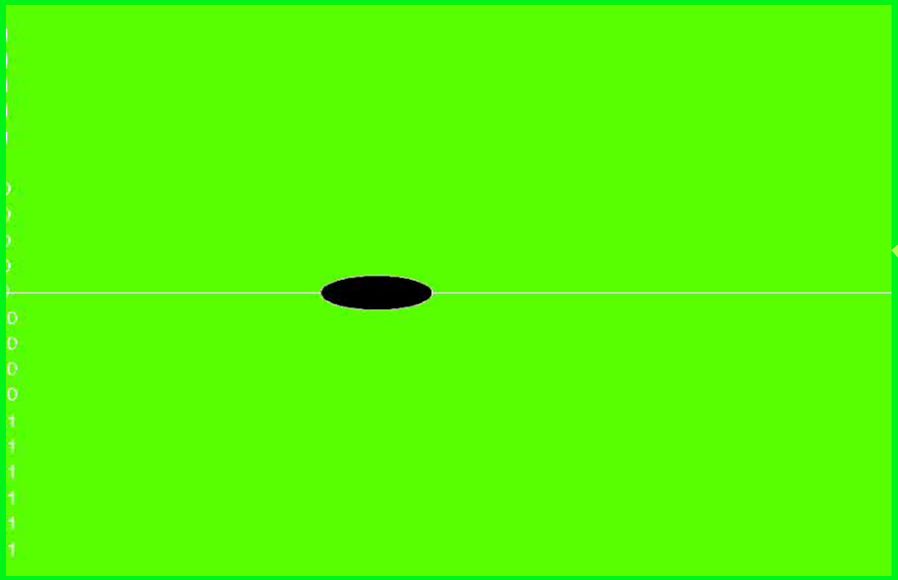
Vorticity field

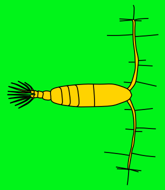



Time-averaged vorticity

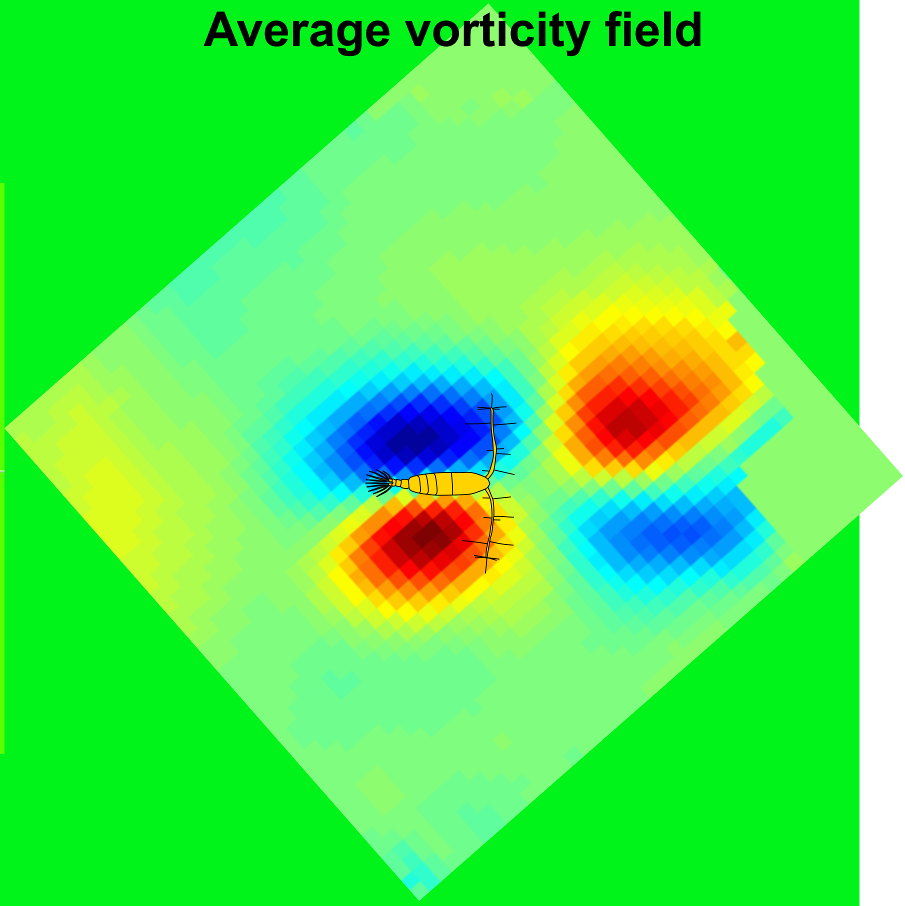
Vorticity field Jump 20-2

CFD simulation



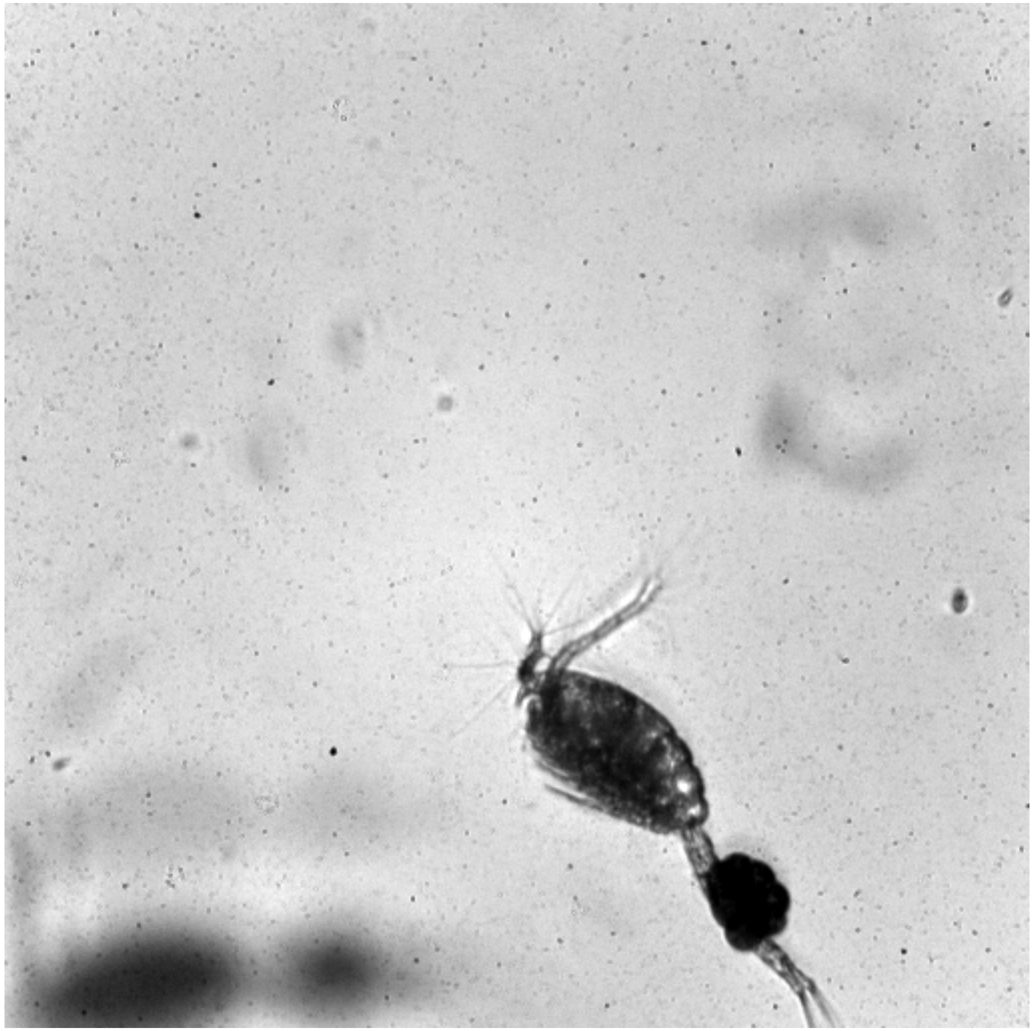


Average vorticity field



Jiang & Kiørboe JEB 2010

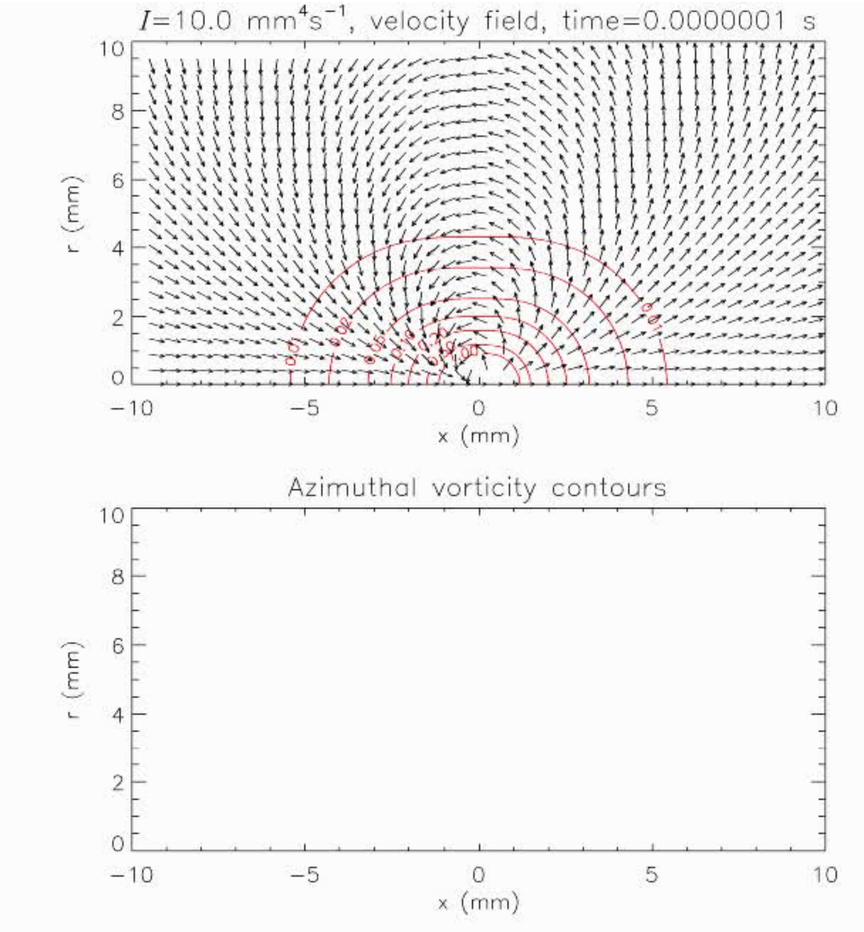
Repositioning jump: Impulsive force



SloMo
Duration of power stroke
is a few ms

2 mm

Analytical model of the wake vortex: Impulsive Stokeslet



Flow field

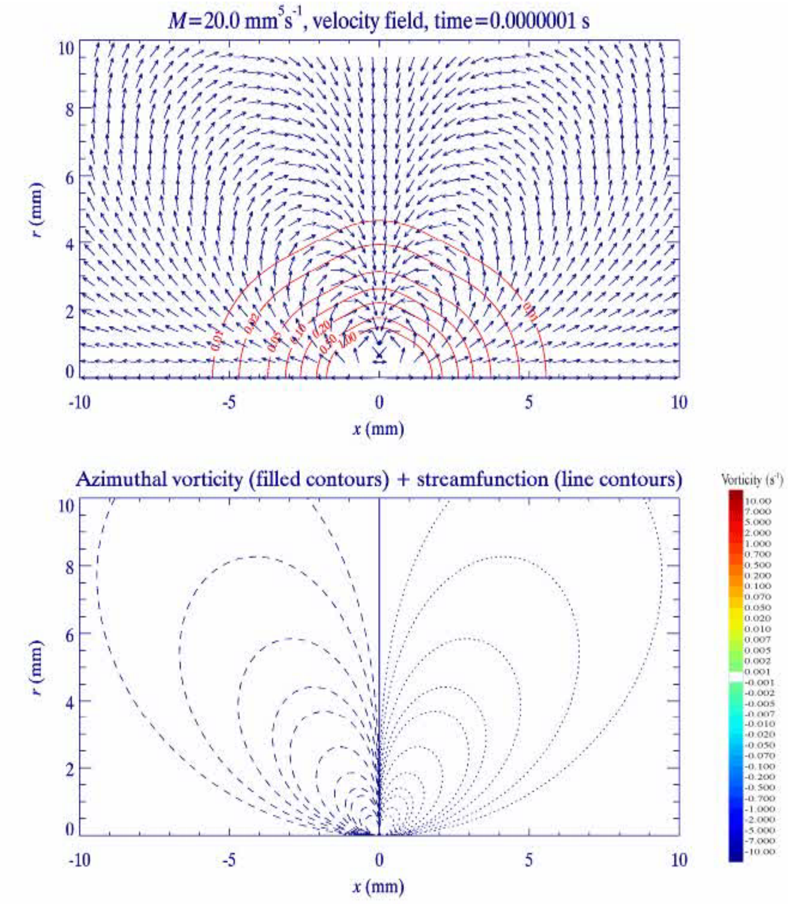
Characterized solely by the Impulse: the momentum imparted to the fluid by the power kick of the copepod (and viscosity) (~ mass x speed of copepod)

Vorticity field

Impulsive stokeslet

Kiørboe et al. Proc. Roy Soc B 2010

Analytical model of the entire flow field: Impulsive stresslet



Two counter-rotating viscous vortex rings of same intensity

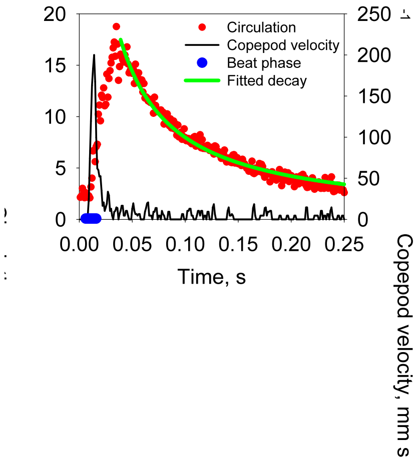
Flow field

Vorticity field

Characterized solely by the strength of the stresslet: ~ the product of speed, mass, and jump distance

Model predicts decay of the vortex

$$\Gamma(t) = \frac{I}{4\pi\nu(t-t_0)}$$



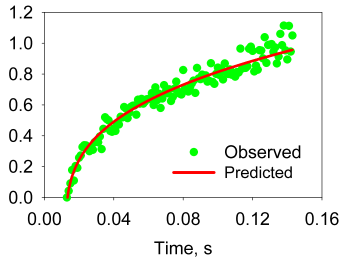
Estimated momentum of wake: 10^{-8} kg m s^{-1}

Circulation: spatial integral of vorticity

Kiørboe et al. Proc. Roy Soc B 2010

Model predicts translation of vortex

$$L(t) = \left(2\nu(t - t_0) + \left(\frac{2I}{\pi}\right)^{1/2} (t - t_0)^{1/2}\right)^{1/2}$$



Kiørboe et al. Proc. Roy Soc B 2010

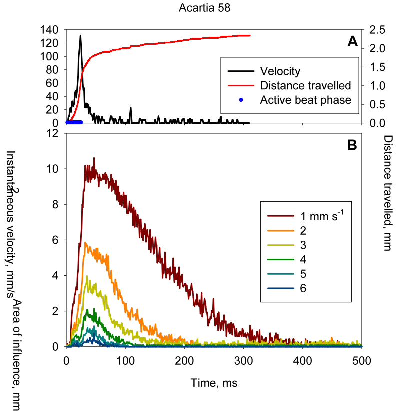
Extension and duration of fluid signal

Extension and duration of fluid signal is a simple function of the speed and mass of the copepod

$$R = f(v, U^*, size)$$

Area of influenc

Extension and duration of fluid signal



$$Area \propto (I/U^*)^{2/3}$$

$$t^* = \frac{1}{4\nu\pi}\left(\frac{2}{3}\frac{I}{U^*}\right)^{2/3} \sim Area$$

Kiørboe et al. Proc. Roy Soc B 2010

Detection distance (*R*) to predator with signal sensitivity *U**

Ambush feeder:

$$R_A = 1.23 \cdot a \left(\frac{v_j}{U^*} \right)^{1/3}$$

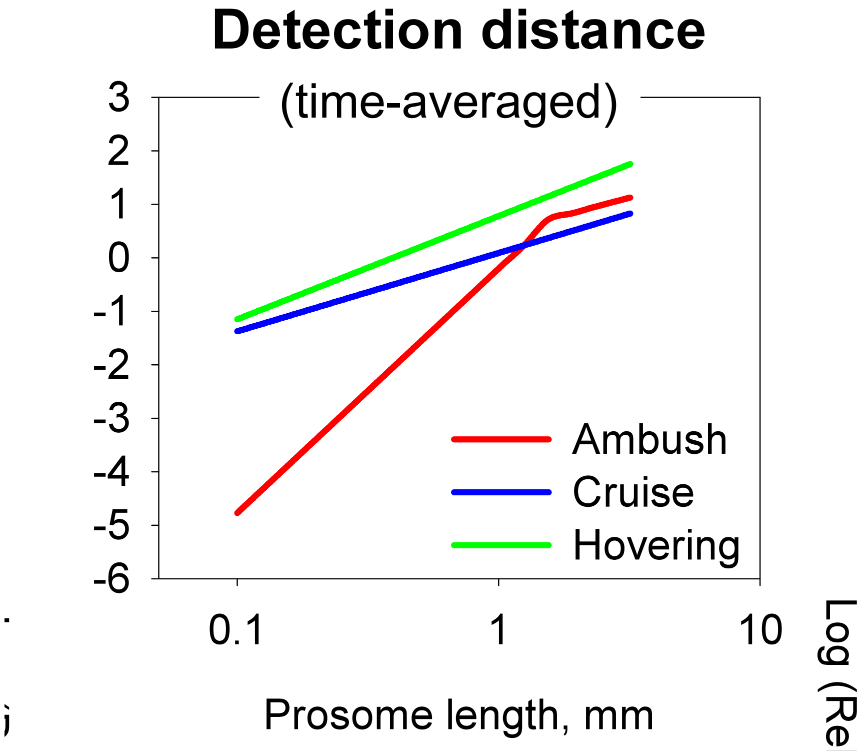
Detection distance to predator with signal sensitivity s^* for the principal feeding modes

Ambush feeder: $R_A = \frac{4}{3} \cdot a \left(\frac{v_j}{s^*} \right)^{1/3}$ $\overline{R_A} \approx a^3 \frac{v_j}{s^*}$

Cruise feeder: $R_C = a \left(\frac{v}{s^*} \right)^{1/2}$ (Force dipole)

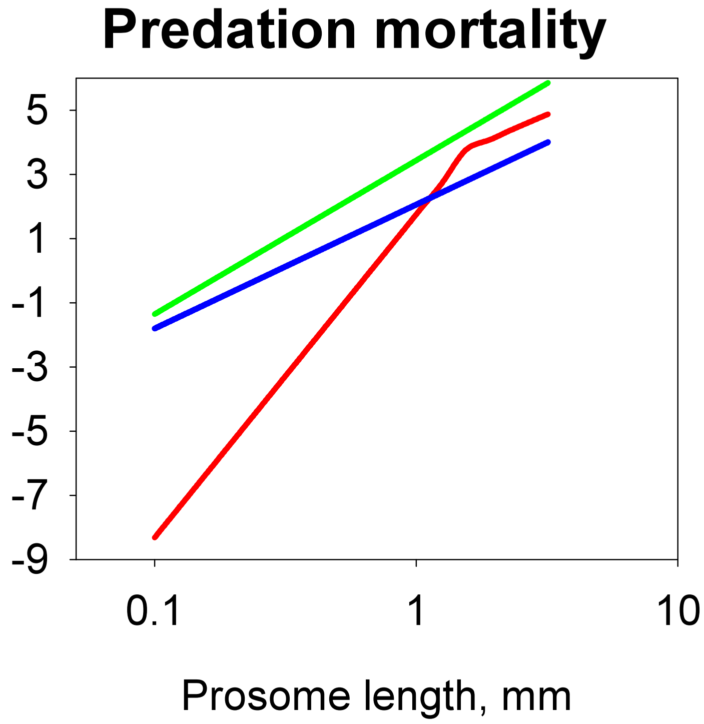
Feeding current feeder:
(Hovering) $R_H = a \left(\frac{v}{s^*} \right)$ (Stokeslet)

Detection distance and predation mortality



Detection distance

$$\pi R^2 \Delta u$$



Predation mortality

Predation risk: AMBUSH < CRUISE < HOVERING

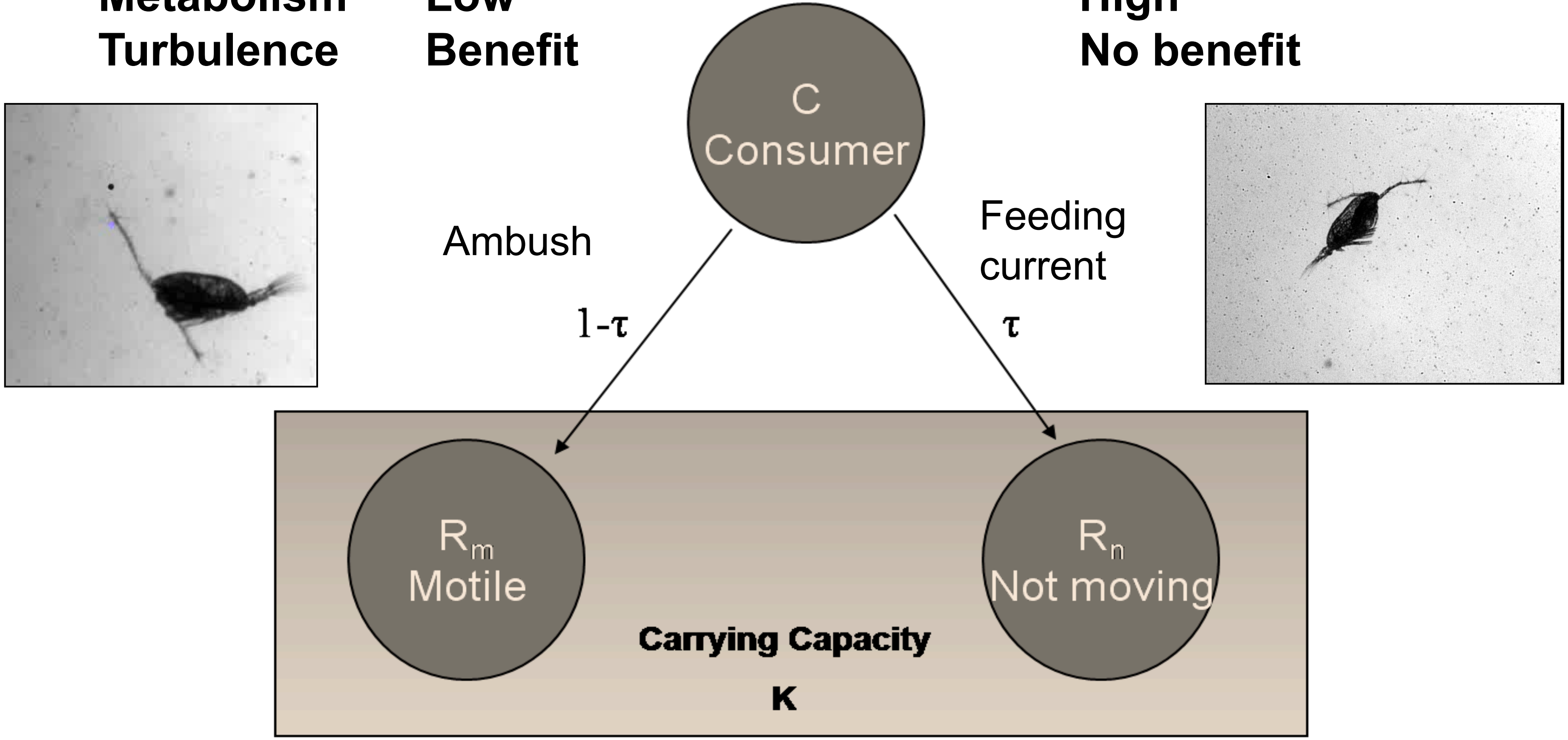
Feeding efficiency: AMBUSH < CRUISE < HOVERING

III. TRAIT BASED MODELLING

A simple example

A trait based model: Adaptive feeding

	AMBUSH	Feeding current
Mortality	Low	High
Metabolism	Low	High
Turbulence	Benefit	No benefit

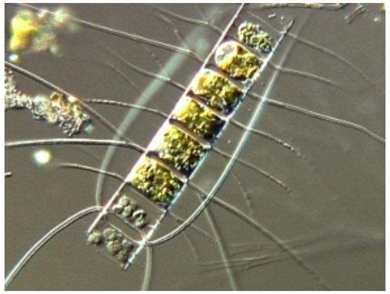


Mariani et al. submitted

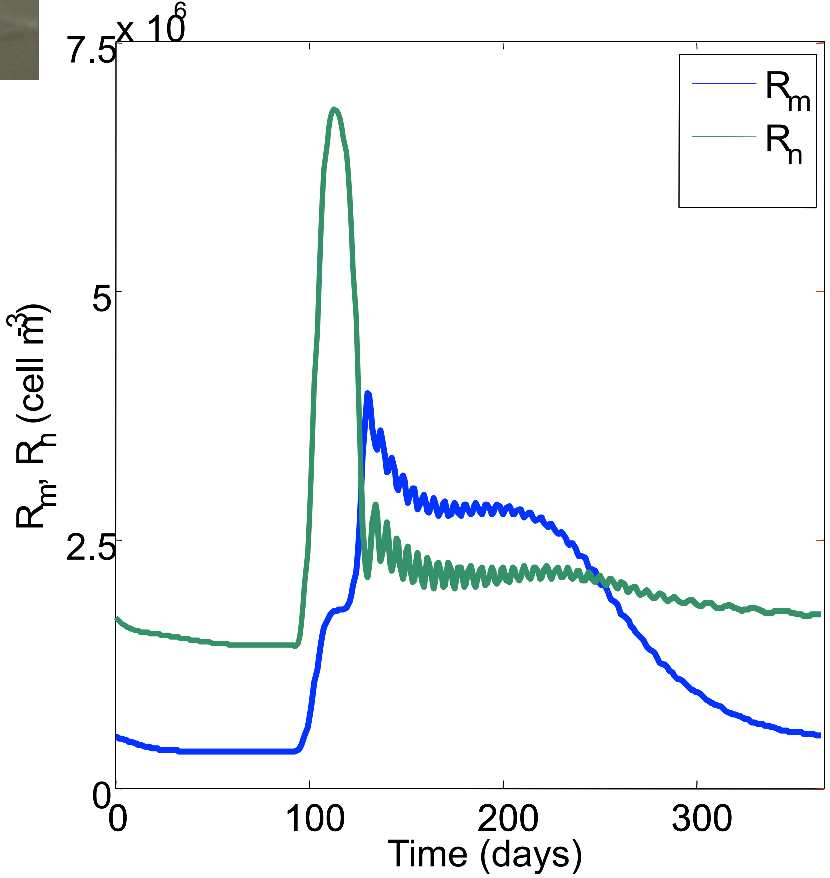
Dynamic adaptation

- The grazer adopts the feeding mode that at any instant maximizes its fitnes defined as **net energy intake/mortality rate**
- Model driven by seasonal variation in light and turbulence (North Sea)

Seasonal succesion of phytoplankotn



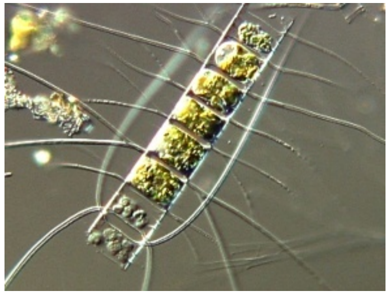
From non-motile diatioms
to motile dinoflagellates



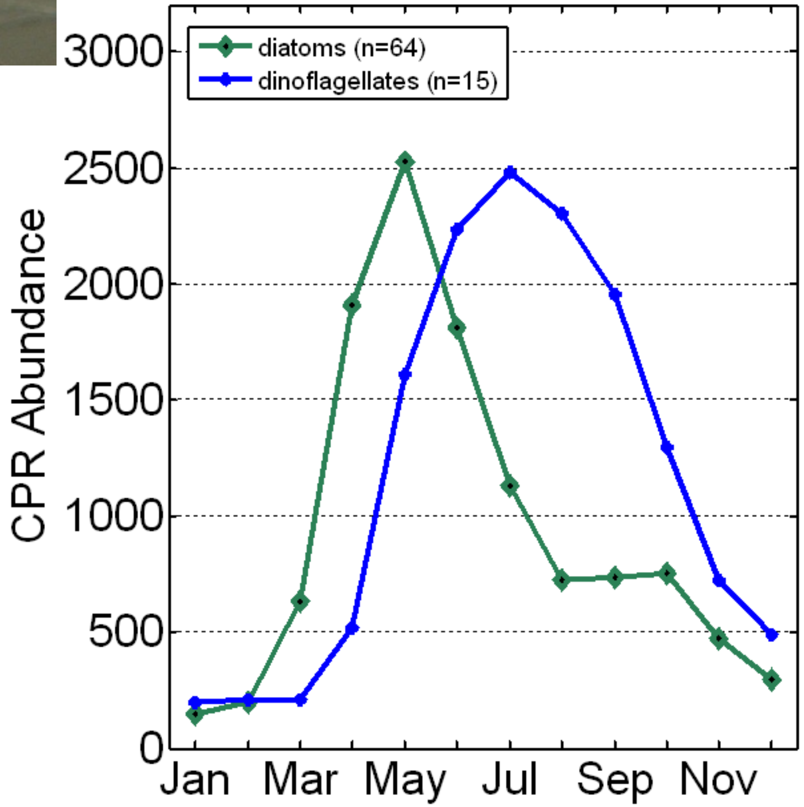
Predicted pattern
North Sea

Mariani et al. submitted

Seasonal succesion of phytoplankotn



From non-motile diatioms
to motile dinoflagellates



Average pattern
N-Atlantic,
CPR survey

Mariani et al. submitted

Take home

- Despite the huge diversity of zooplankton, there are few principal ways of solving the 3 main missions of life
- These can be described mechanistically and mathematically, thus allowing predictive models of behavior
- From a mechanistic understanding of the traits we may be able to deduce the trade offs
- **Trait-based models** may be an efficient tool to describe and predict the dynamics of pelagic ecosystems

Acknowledgements

HH Jakobsen
A Andersen
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S Colin