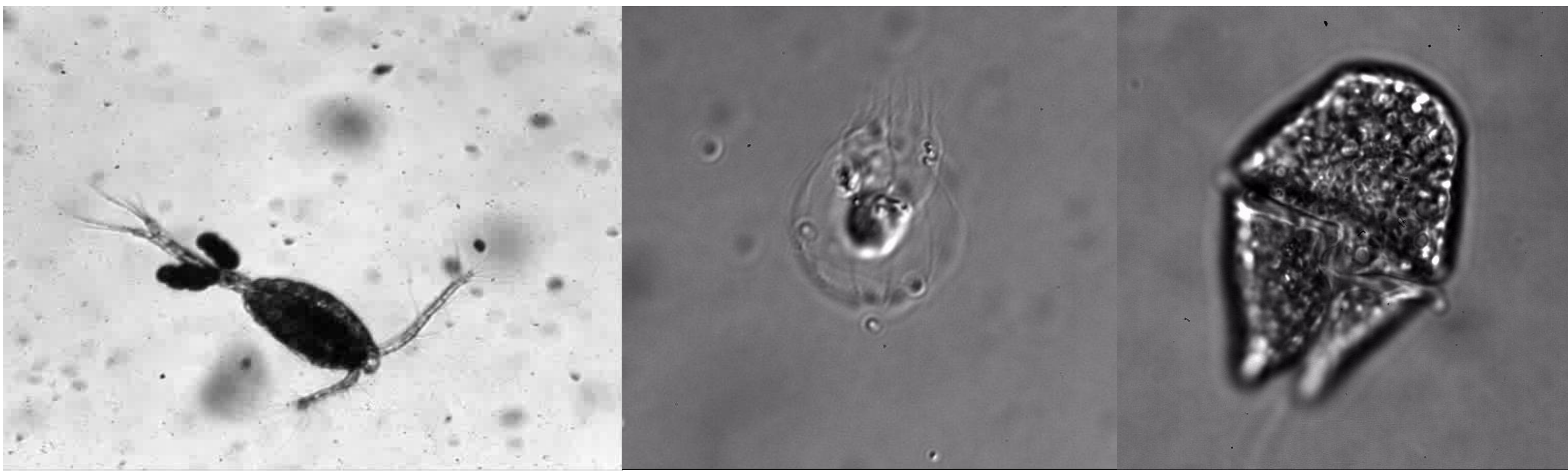
Ocean Life
Centre for Ocean Life
VKR Centre of Excellence

MYSTERIER, MYTER OG ANDRE HISTORIER OM HAVETS MIKROSKOPISKE LIV



Thomas Kiørboe
Centre for Ocean Life, DTU Aqua

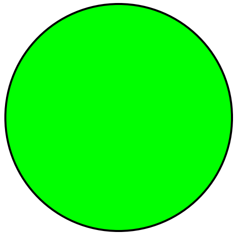
Vand forekommer så tykt som sirup

Små vanddyr lever i en underlig verden

Taylors forsøg

Vand er så tykt som sirup

Grib ud efter et æble



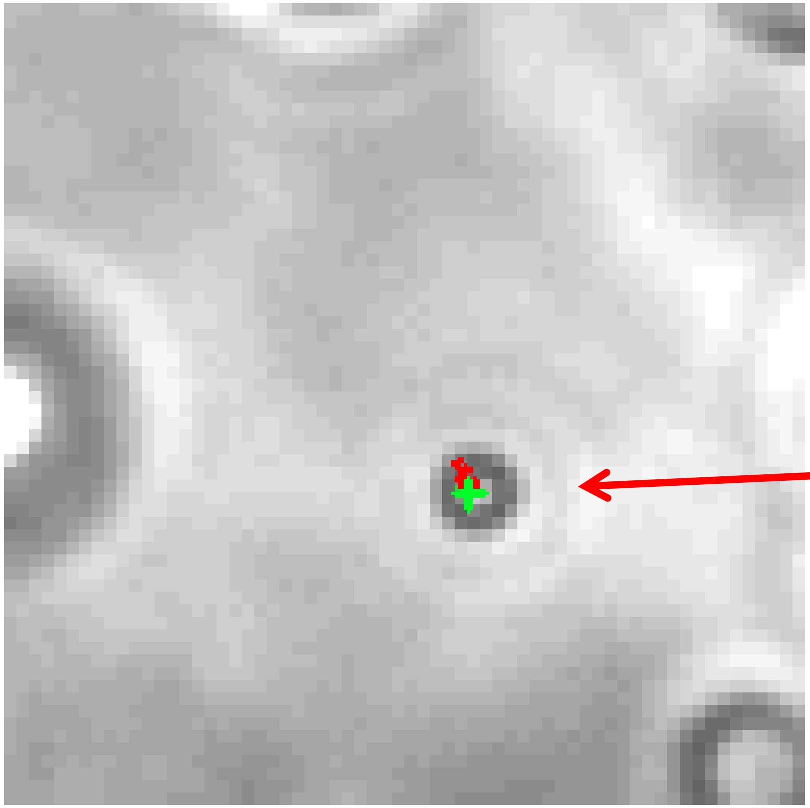
Æble

Frustration!

Vand er så tykt som sirup

Problem: Byttet skubbes væk

Paraphysomonas sp
An interception-feeding flagellate



Prey

Slow motion

Courtesey
Ray Goldstein

5 mysterier og myter

Svar på 5 spørgsmål i aldrig har stillet

1. Myte: copepoder kan lugte deres bytte på stor afstand

2. Mysterium: kravefalgellatens flagel-pumpe er 100x for svag

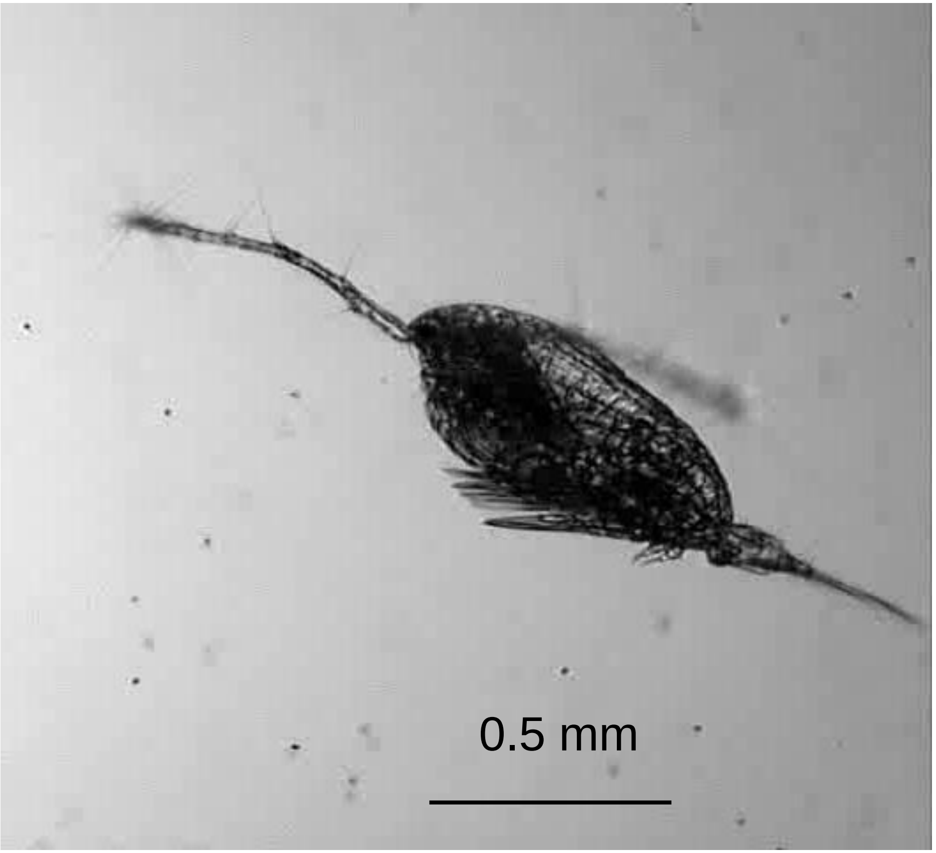
3. Mysterium: Hvordan kan en copepod springe mod sit bytte uden at skubbe det væk?

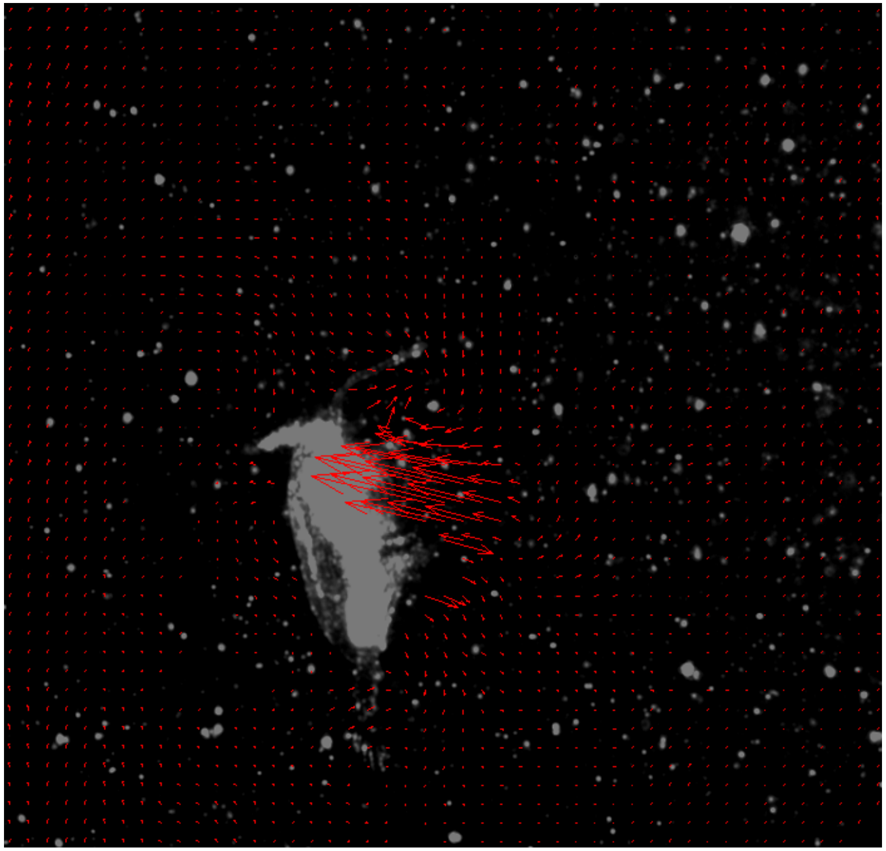
4. Mysterium: hvorfor snurrer dinoflagellater den forkerte vej?

5. Hvordan gemmer plankton sig?

I: ‘Filter feeding’ copepopods

The feeding current is a scanning current – NOT a filtering current





Acartia tonsa beating its feeding appendags to generate a feeding current

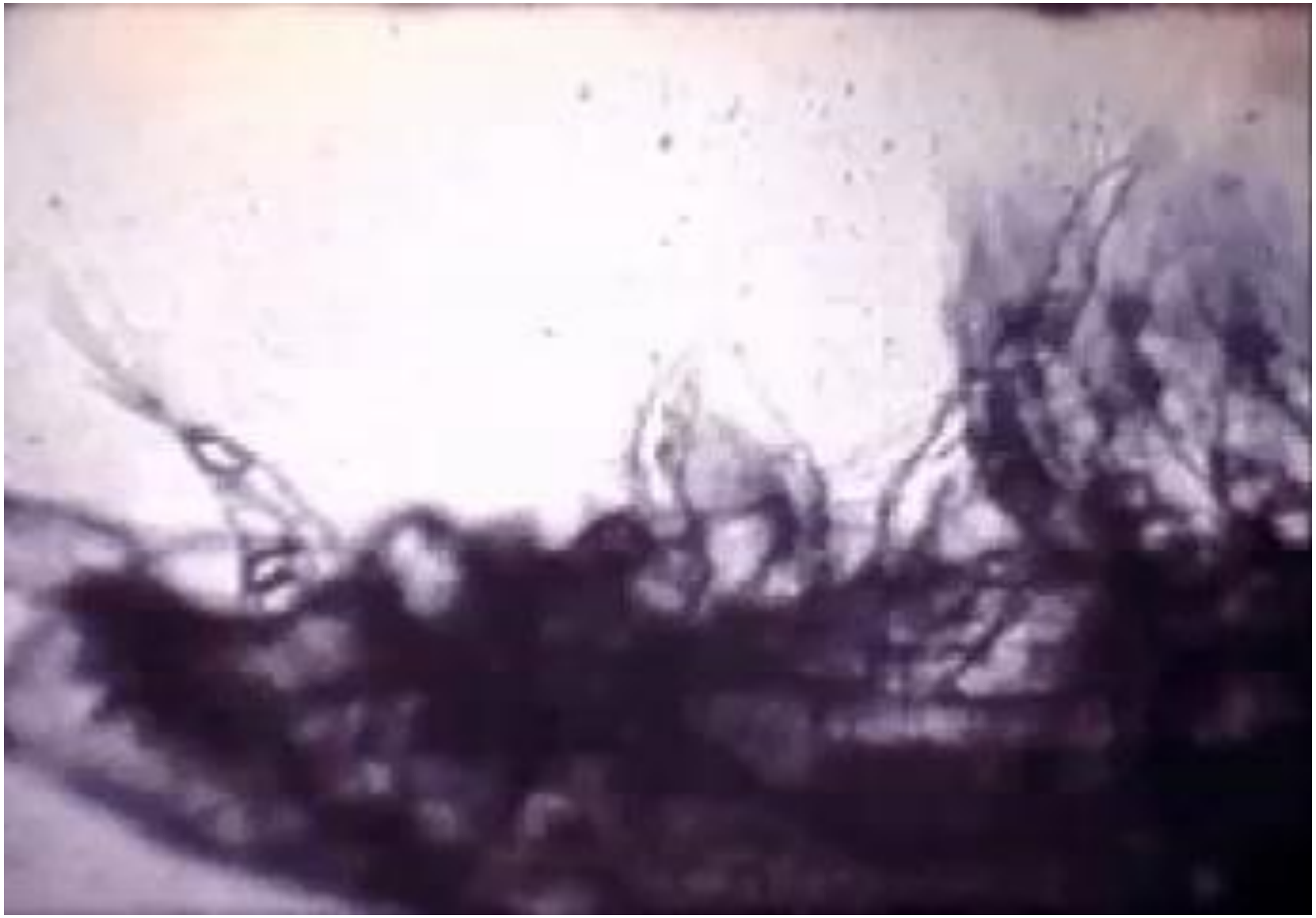
SloMo 1:40

Pioneerne

Strickler, Paffenhöfer og Acaraz i arbejde

Pioneerne

Capturing the algae



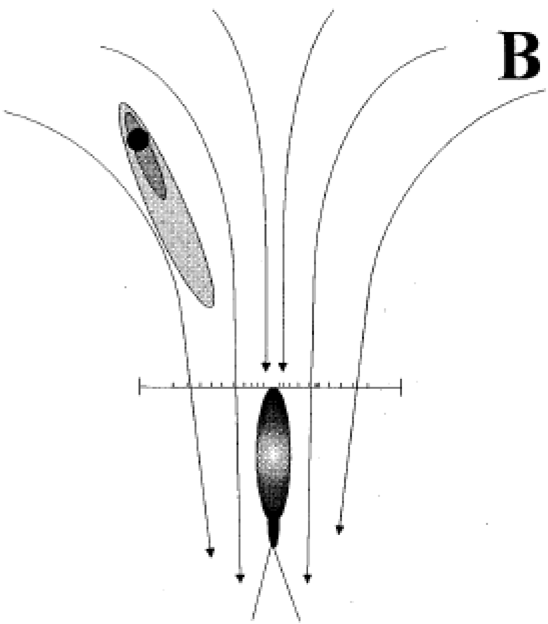
Eucalanus pileatus SloMo

Strickler movies

Never believe an observation until verified by a model

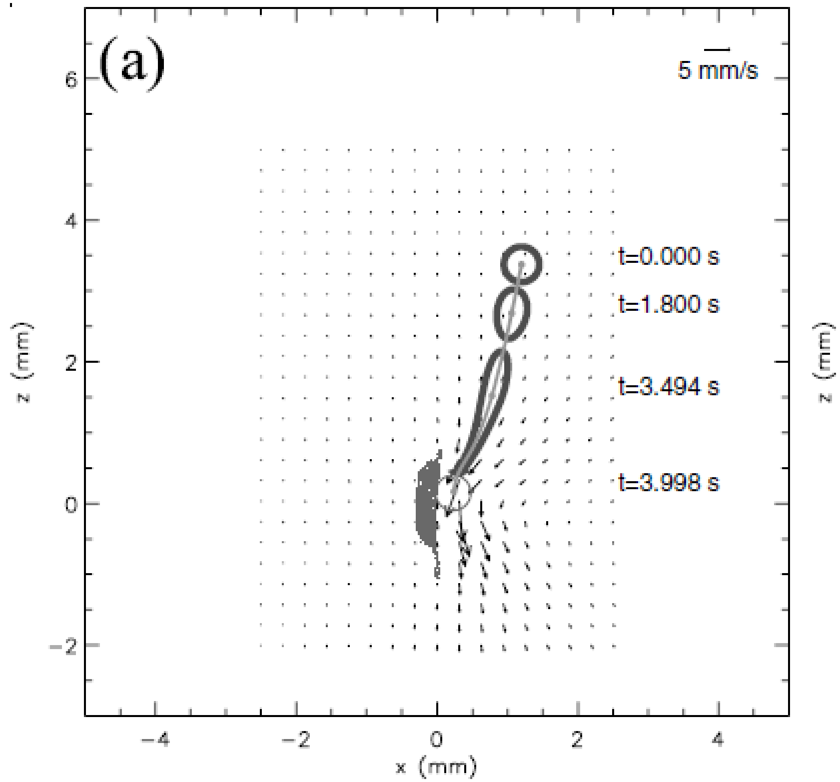
Andrews (1983) and Jiang et al. (2001)

Andrew's (1983) model



Moore et al. *L&O* 1999

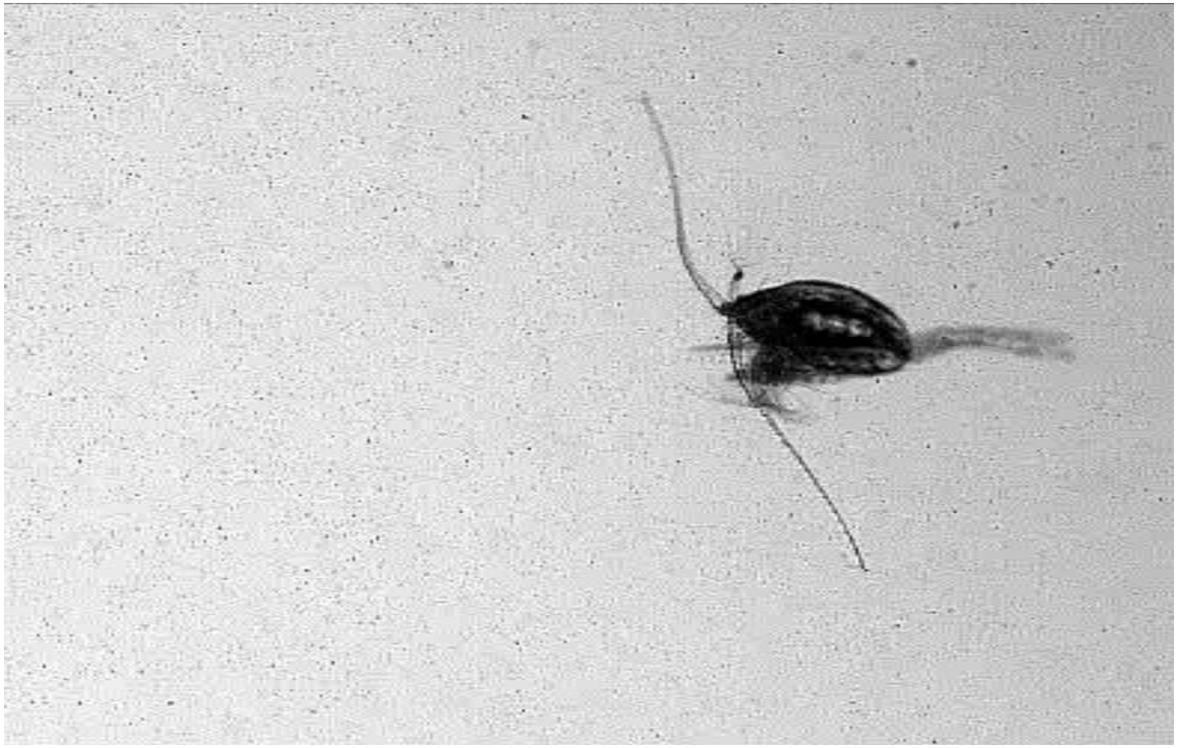
Jiang's CFD predict 1 body length detection distance and 500 ms lead time

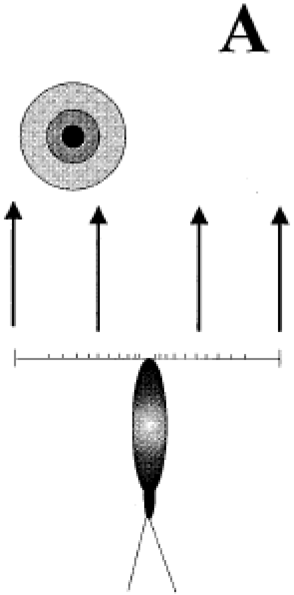


Jiang et al. *JPR* 2001

What about cruise feeders?

Many copepods cruise through the water without a feeding current



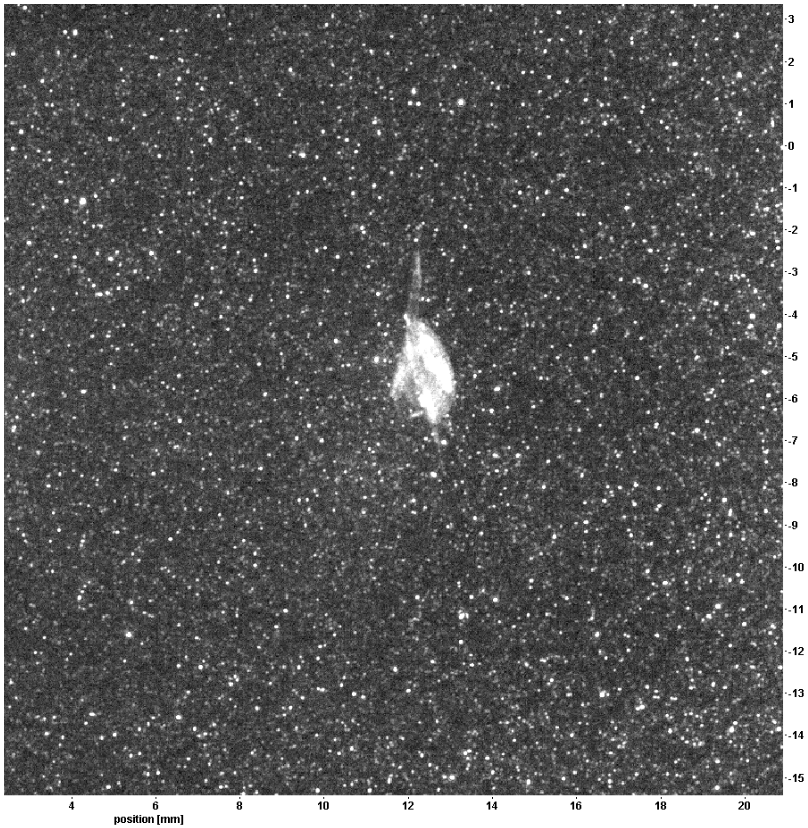


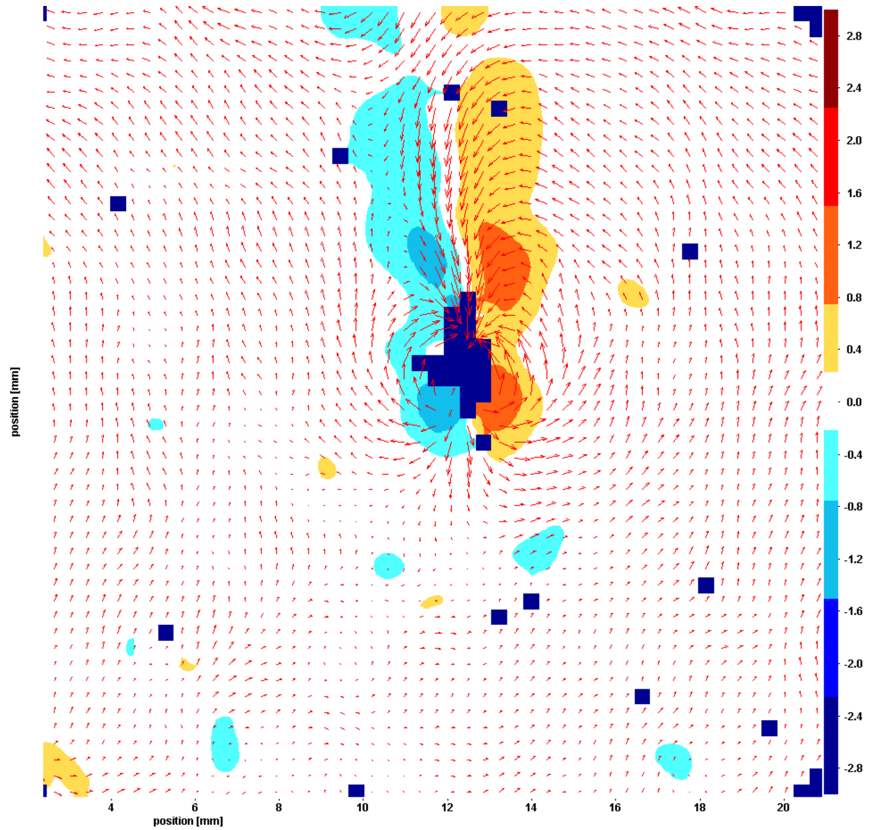
Moore et al. L&O 1999

Metridia longa cruising through the water
(Kjellerup & Kiørboe *Biol Lett* 2012)

Cruising: *Metridia longa*

Flow and vorticity fields





Kjellerup & Kiørboe *Biol Lett* 2012

SloMo 1:7

Cruise feeding: *Metridia longa*

Non-motile prey perceived by tacticle or gustatory cues

SloMo 1:50

Kjellerup & Kiørboe *Biol. Lett*. 2012

Feeding current feeding: *Paracalanus parvus*

Non-motile prey perceived by tacticle or gustatory signals

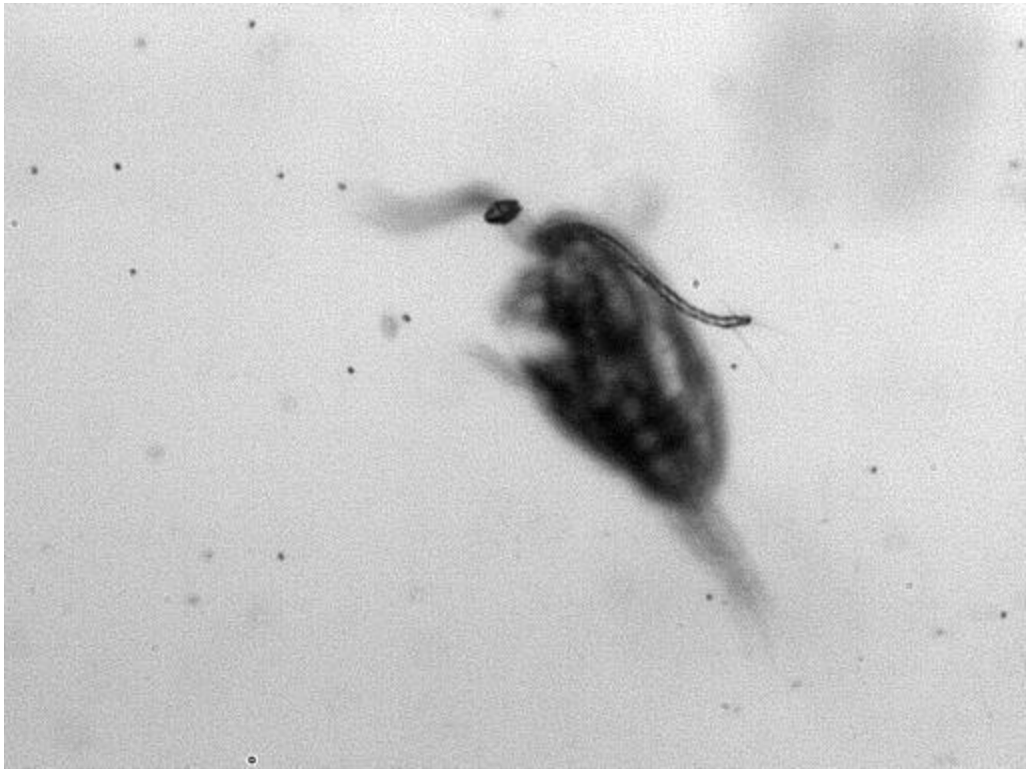
Feeding current (SloMo 1:20)

Capture of arriving cell (SloMo 1:80)

Tiselius et al *LO* 2013

Feeding current feeding: *Paracalanus parvus*

Even very large cells are perceived only upon direct contact

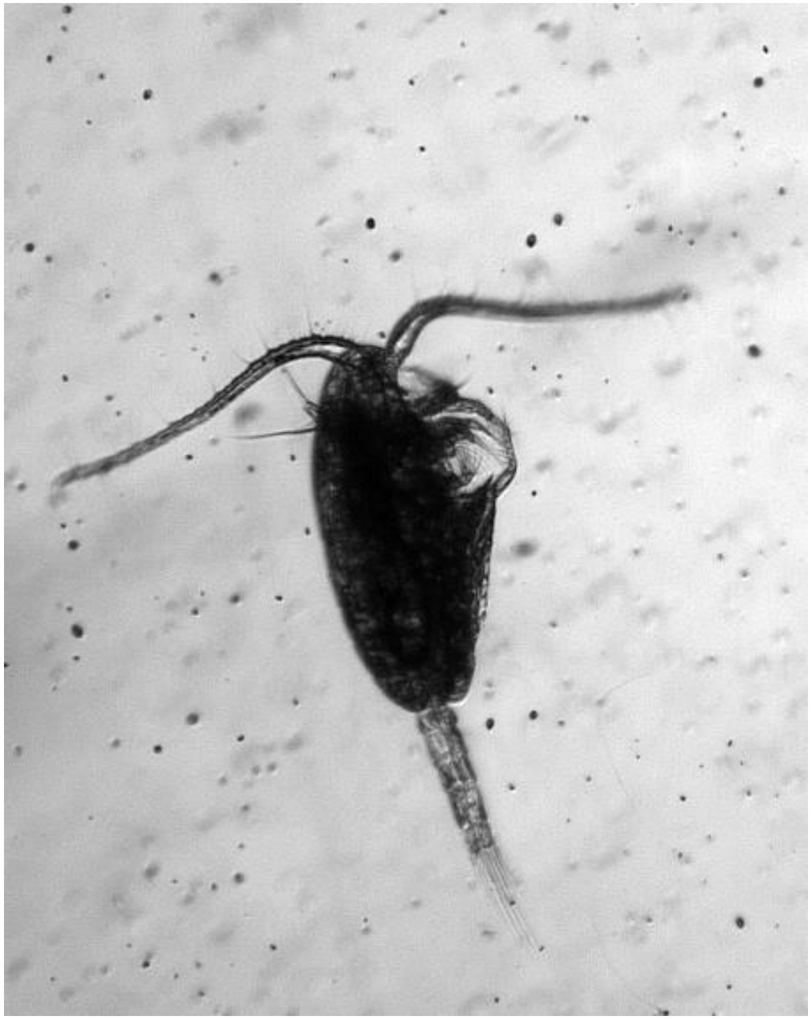


0.1 mm

Tiselius et al *LO* 2013; SloMo 1:10

Feeding current feeding: *Pseudocalanus* sp

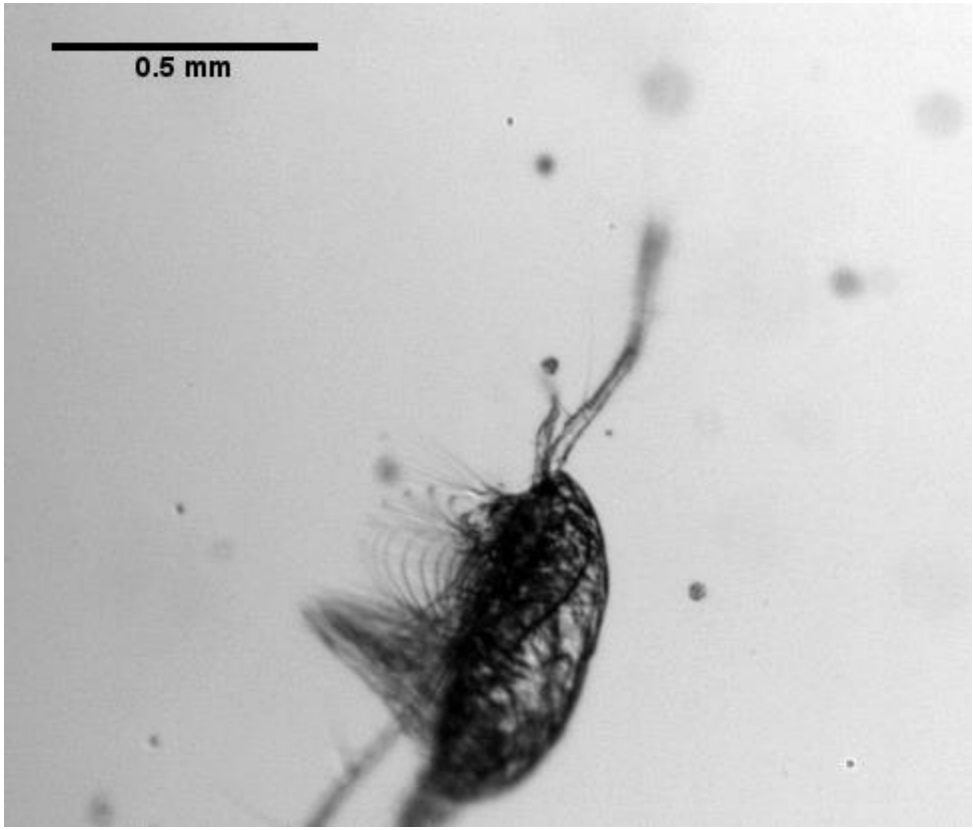
Non-motile prey perceived by tacticle or gustatory signals

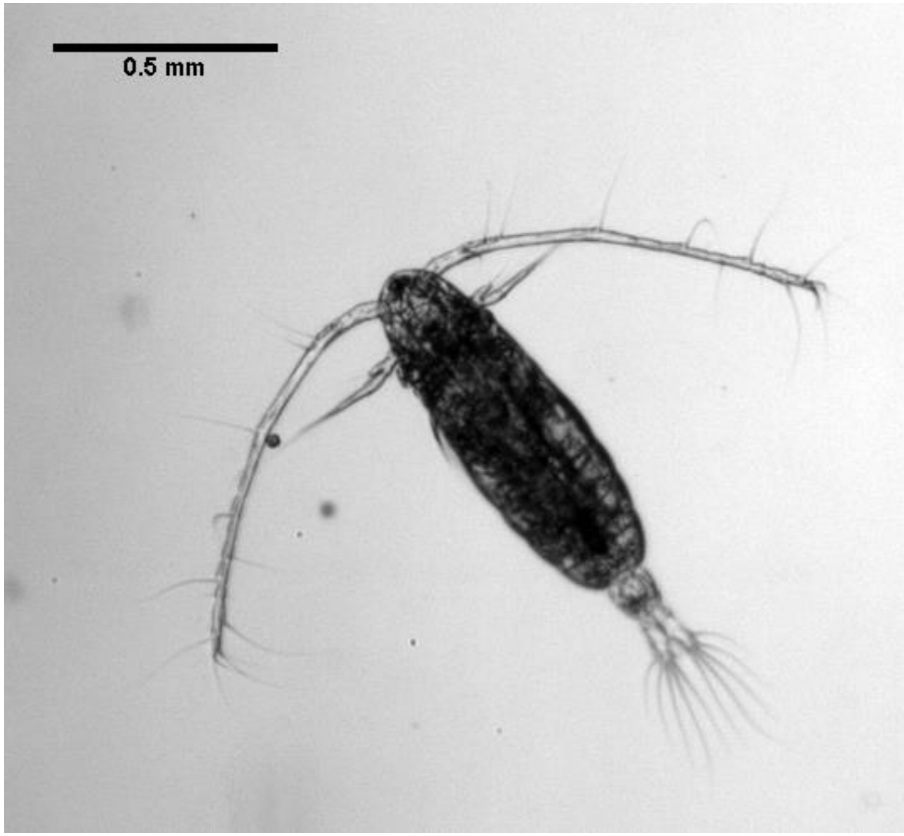


Tiselius et al *LO* 2013

Feeding current feeding: *Acartia tonsa*

Non-motile prey perceived by tacticle or gustatory signals

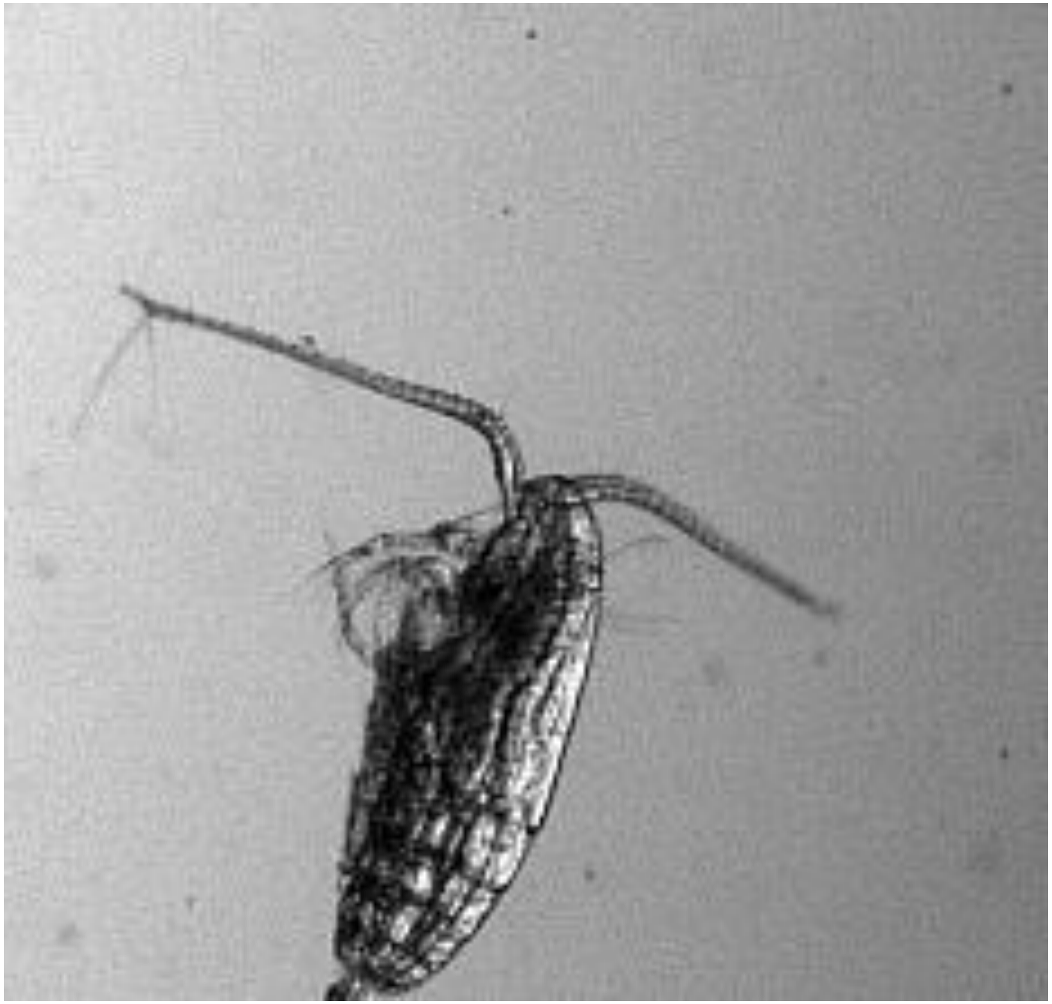




SloMo 1:50

Feeding current feeding: *Calanus helgolandicus*

Non-motile prey perceived by tacticle or gustatory signals

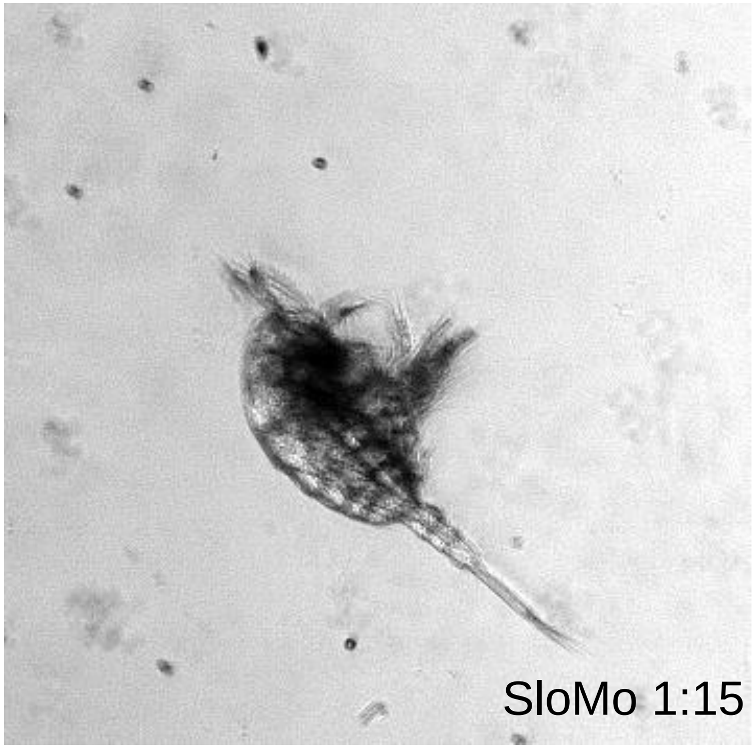


Feeding current feeding: *Temora longicornis*

Non-motile prey perceived by tacticle or gustatory signals

Feeding on phytoplankton (*Linguloidiniums*)

Feeding on plastic beads



Same capture response, different result of 'tasting'

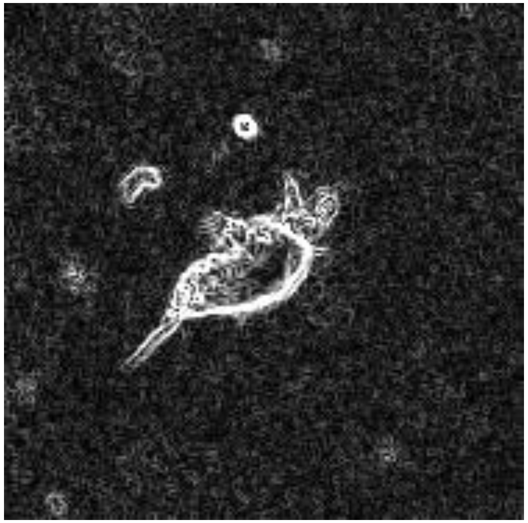
Gonçalves et al. MEPS 2014

Feeding current feeding: *Temora nauplii*

Non-motile prey perceived by tacticle or gustatory signals

Feeding on phytoplankton (*Rhodomonas*)

Feeding on plastic beads



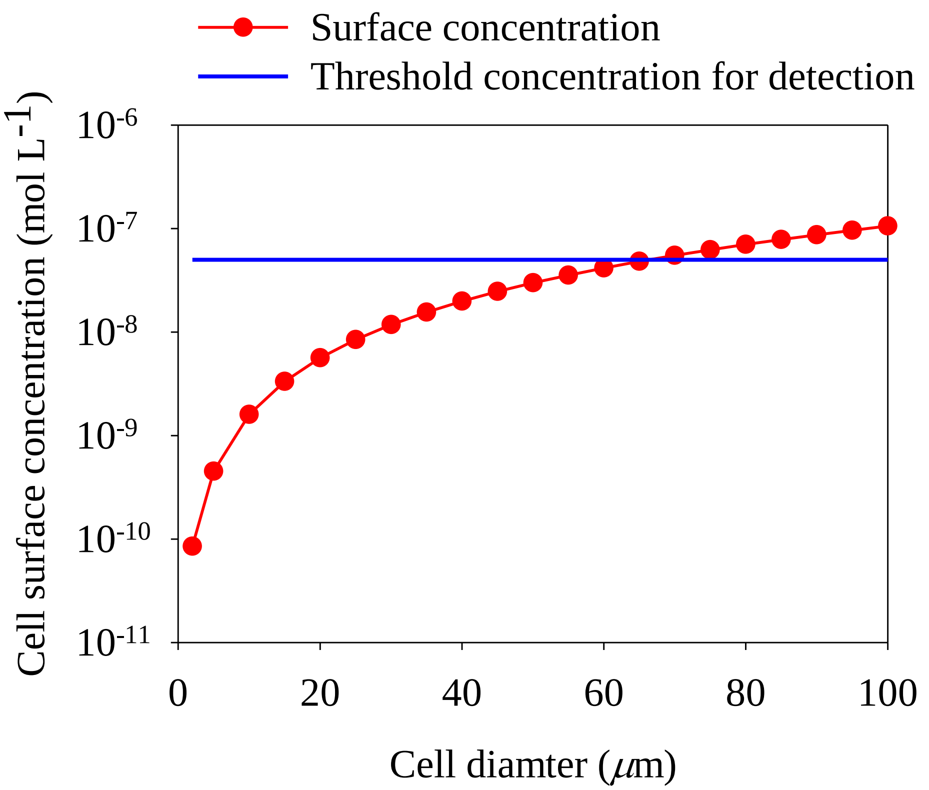
Same capture response, different result of 'tasting'

Bruno et al. *PlosOne* 2012; Gonçalves & Kiørboe unpublished; Slo:mo

Is remote chemical detection feasible?

Concentration of leaking substances at cell surface

$$C_r = \frac{Q}{4\pi D r} > C_{cr}$$



Assumptions:

- Leakage rate, Q = 5 % d^{-1}
- $C_{cr} = 5*10^{-8}$ M

Conclusion:

- Minimum cell size for chemical detection is about 60 μm.
- Remote detection is only feasible for much larger cells

Tiselius et al *LO* 2013

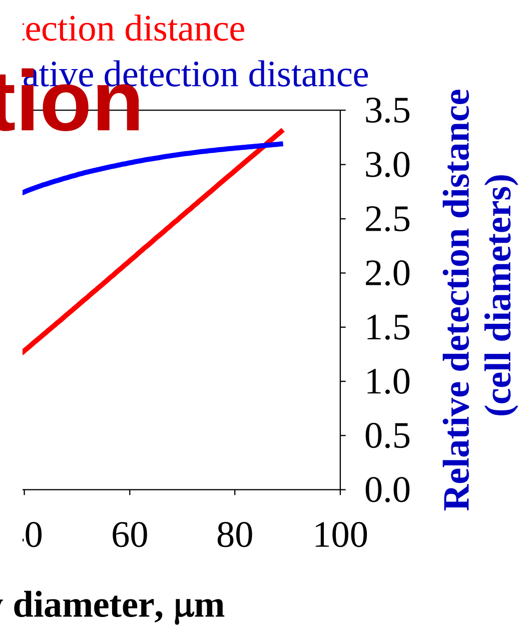
Is hydromechanical detection feasible?

The fluid signal generated by non-motile particle in feeding current

$$R \approx \frac{a}{2}\left[1+\left(1+2\left(\frac{15b^3U}{a^3s}\right)^{1/2}\right)^{1/2}\right]-a$$

YES, it is feasible

Observed and predicted detection distances are consistent



E. pileatus : *U* = 6 mm/s; *a* = 0.5 mm, *s* = 20 μm s^{-1} (Paffenhöfer & Lewis 1990, Yen et al. 1992)

Visser *MEPS* 2001

Is hydromechanical detection feasible?

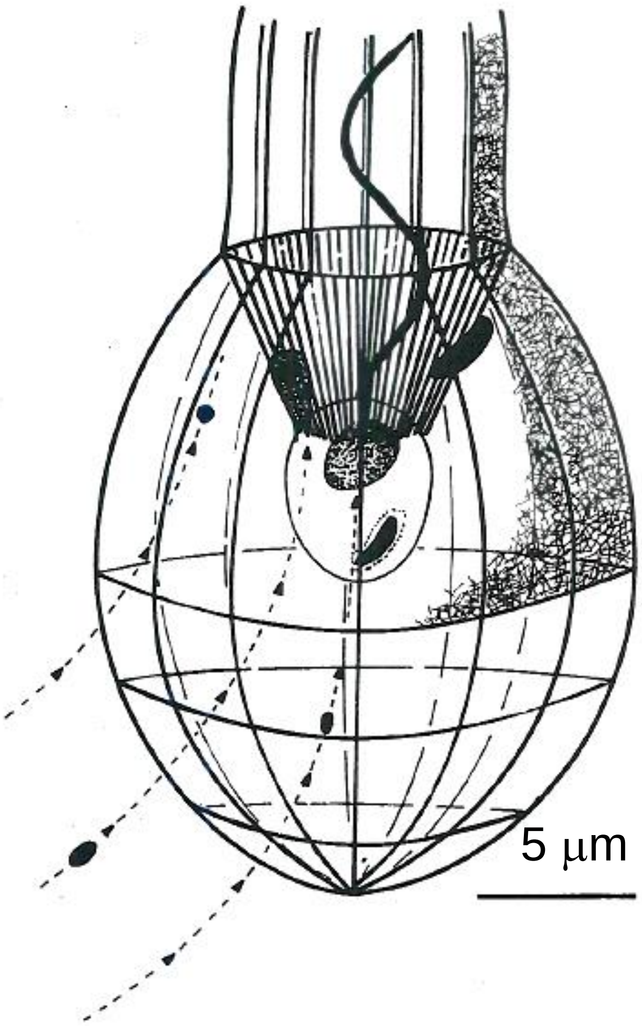
Remote detection: 2-3 prey diamters away

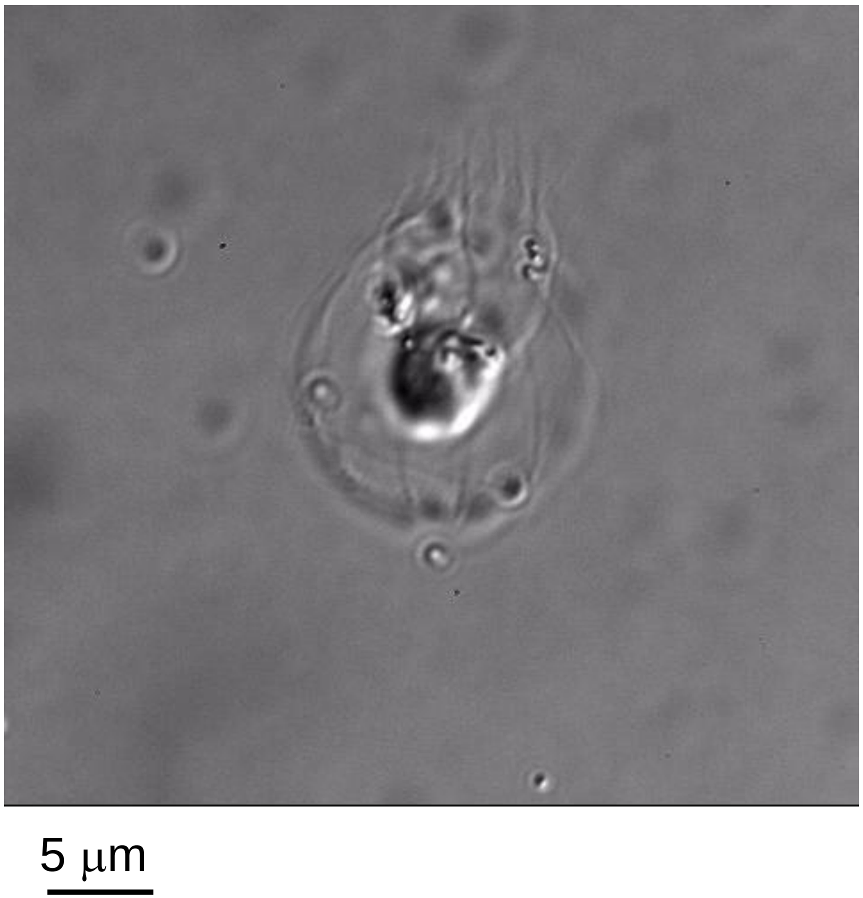
Is hydromechanical detection feasible?

Remote detection: 2-3 prey diamters away

II: Filterfeeding choanoflagellates

I samarbejde med Lasse Tor Nielsen og Anders Andersen

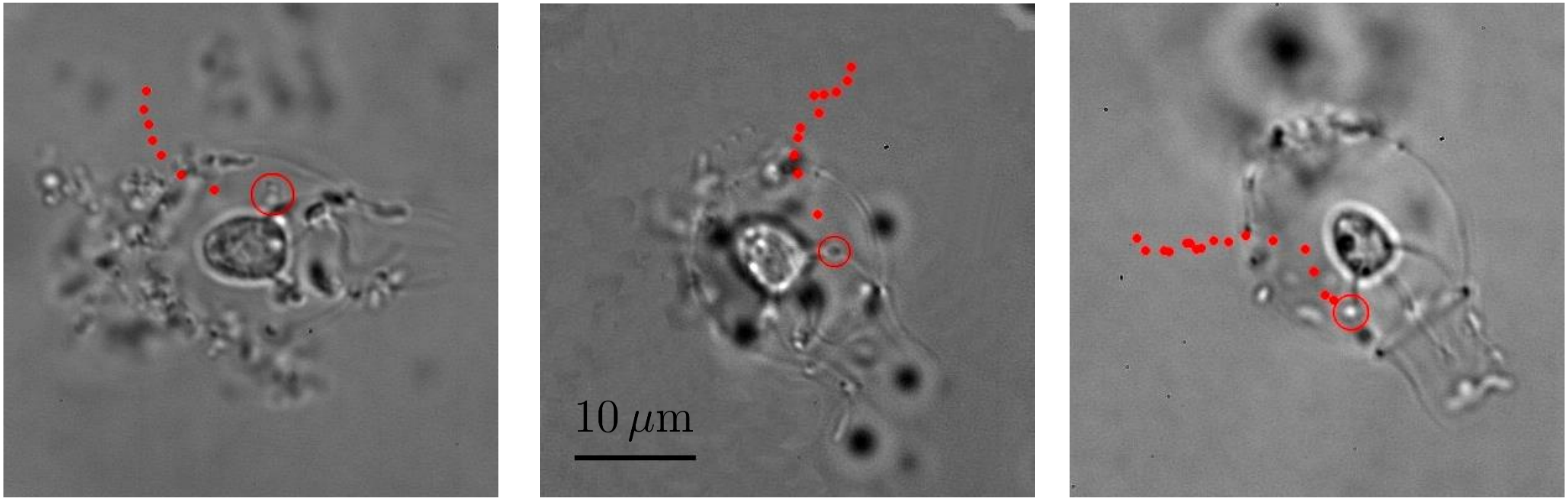




Kraveflagellat æder bakterier

II: Filterfeeding choanoflagellates

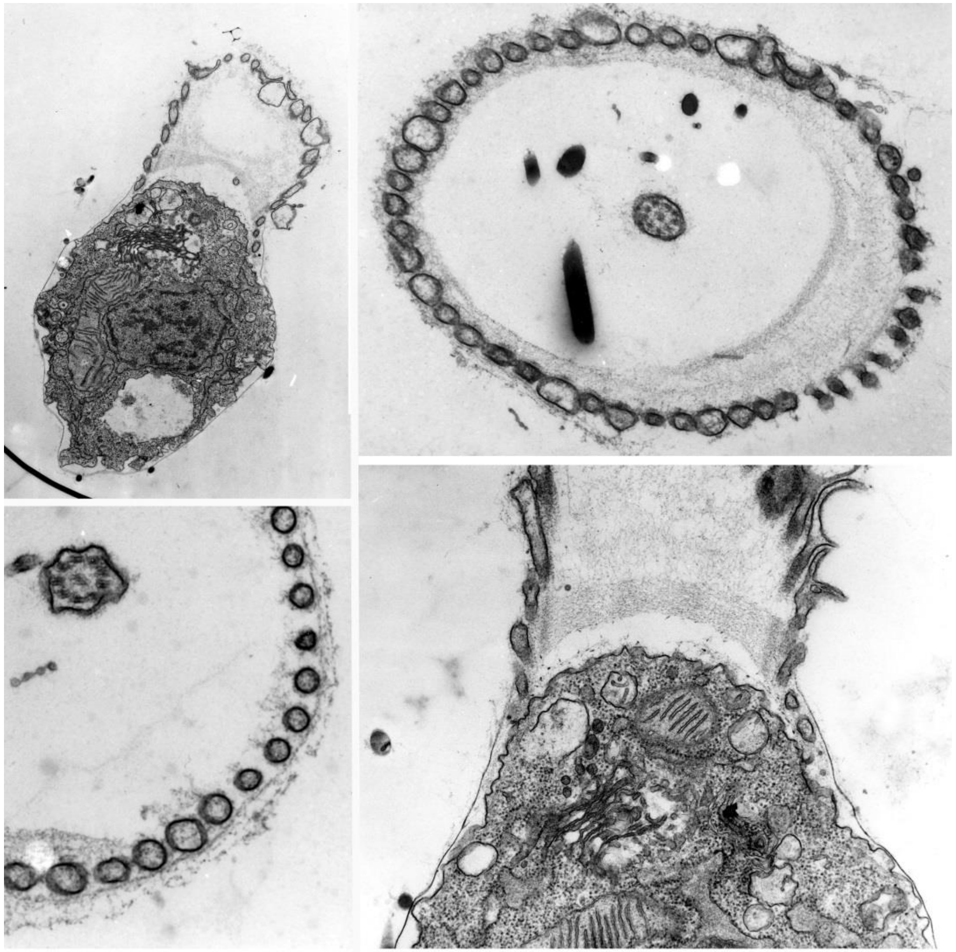
Partikelspor og fangst på filter



Red dots mark particle positions at 0.5 second intervals. Particle velocities immediately before interception are 5-10 micron per second.

Diaphanoeca grandis

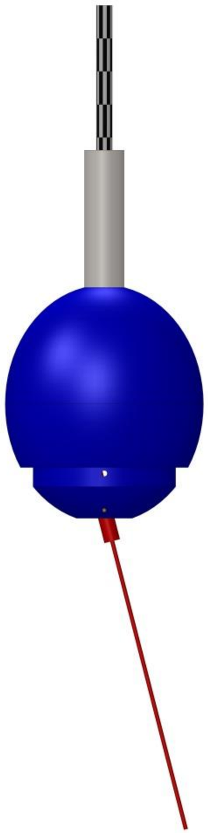
Filter struktur



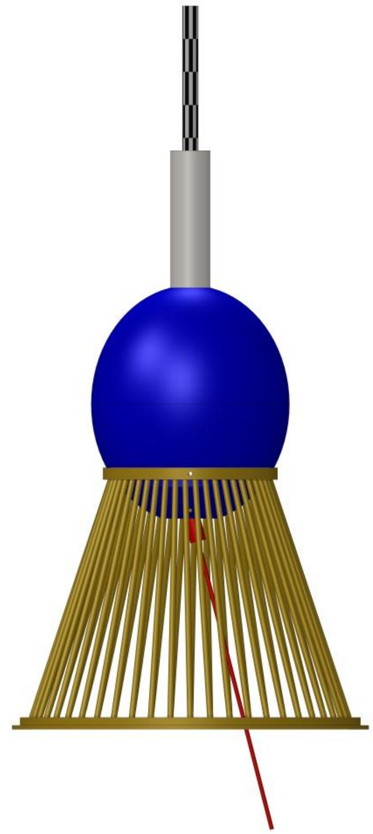
Images by courtesy of Helge Abildhauge Thomsen.

Choanoflagellat

Dynamisk skalerede modeller



Cell and flagellum



Collar filter

Lorica

Choanoflagellat

Dynamisk skalerede modeller

Images by courtesy of Katrine Haaning

Choanoflagellat

Dynamisk skalerede modeller

Film by courtesy of Katrine Haaning

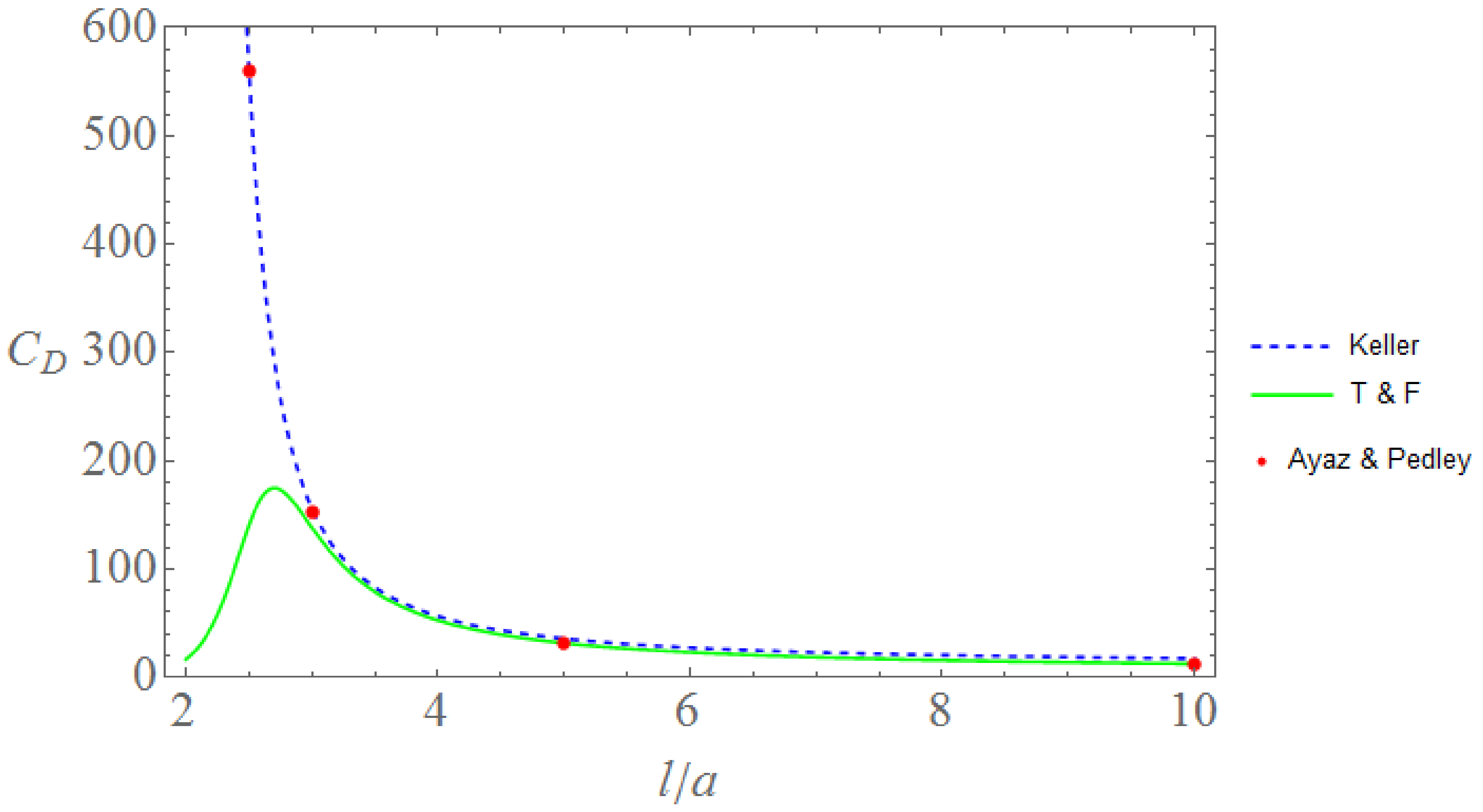
Choanoflagellat

Dynamisk skalerede modeller

Images by courtesy of Katrine Haaning

Modstand i filteret

Drag som funktion af 'maskevidde'



Ayaz and Pedley, Eur. J. Mech. B/Fluids **18**, 173-196 (1999).

Hvor stor kraft producerer flagellen?

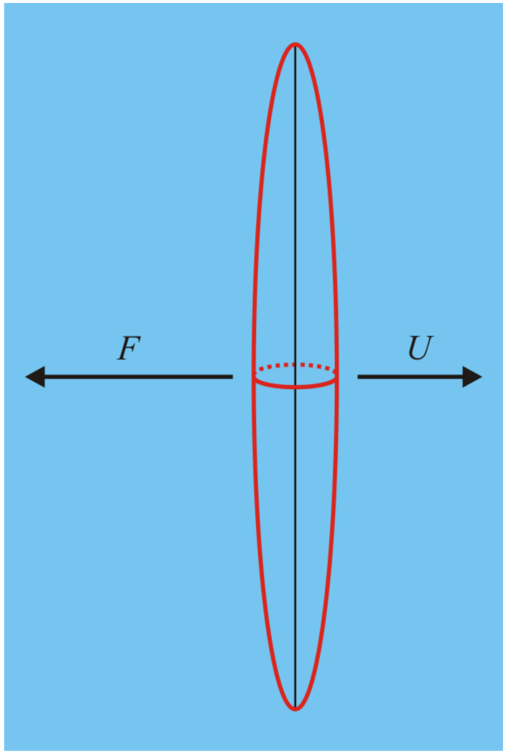
Et simpelt, øvre estimat

Estimate of force as drag on slender spheroid (rod) that is moving sideways:

$$
\begin{aligned}
F &= C_F \, \mu \, L \, U \\
&= 2 \, C_F \, \mu \, L \, A \, f \\
&= 2 \cdot 10^{-12} \, \mathrm{N}
\end{aligned}
$$

$$U = 2 \, A \, f$$

$$C_F = \frac{4 \, \pi}{\ln(2 \, L/b) \, + \, 1/2}$$



Resulterende clerance rate

Hvor meget vand kan flagellen pumpe gennem filtret?

Simple clearance rate estimate taking the filter resistance in to account:

$$Q = \kappa \frac{a}{\mu} F$$

$$= 2\,\kappa\, C_F\, a\, L\, A\, f$$

Teorestisk estimat

$$= 60\,\mu\mathrm{m}^3\mathrm{s}^{-1}$$

Clearance rate inferred from grazing experiments:

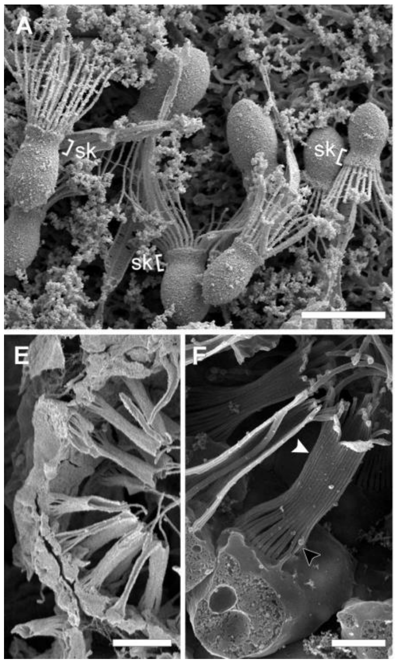
Målt

$$Q = 4.4 \cdot 10^3\,\mu\mathrm{m}^3\mathrm{s}^{-1}$$

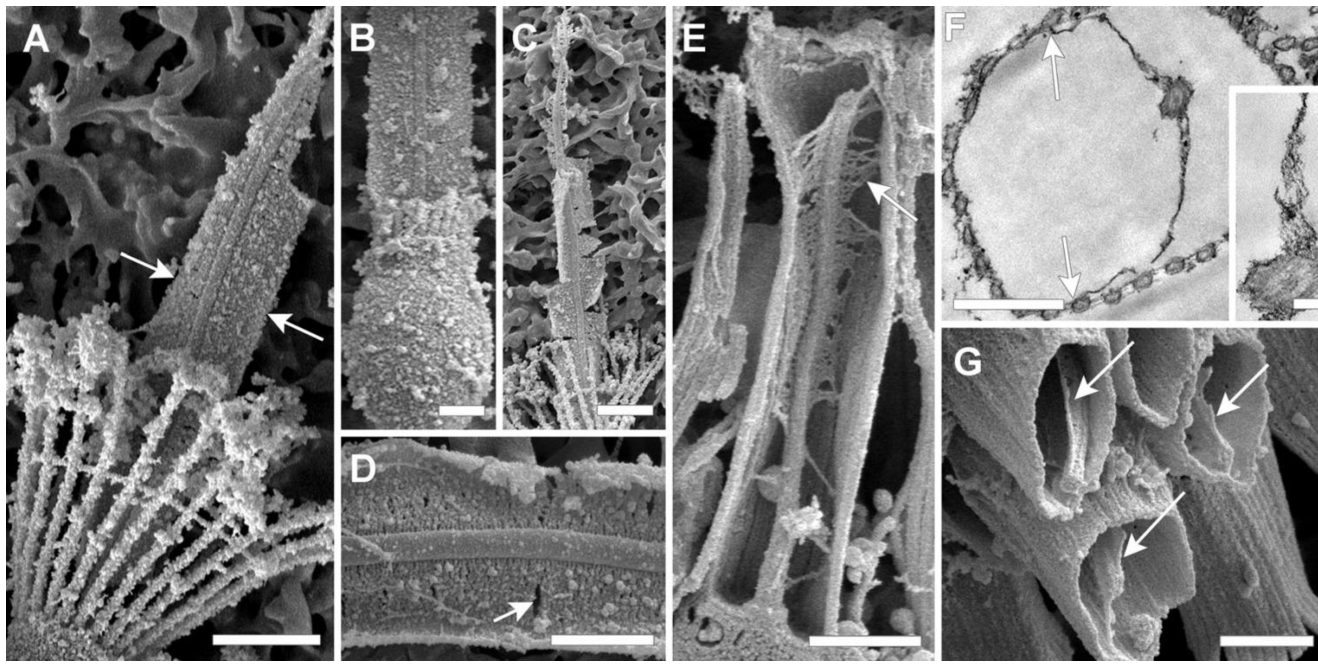
Per Andersen, Marine Microbial Food Webs **3**, 35-50 (1988/1989).

Flageller med sejl

Svampen *Spongilla lacustris* og choanoflagellaten *Monosiga brevicollis*



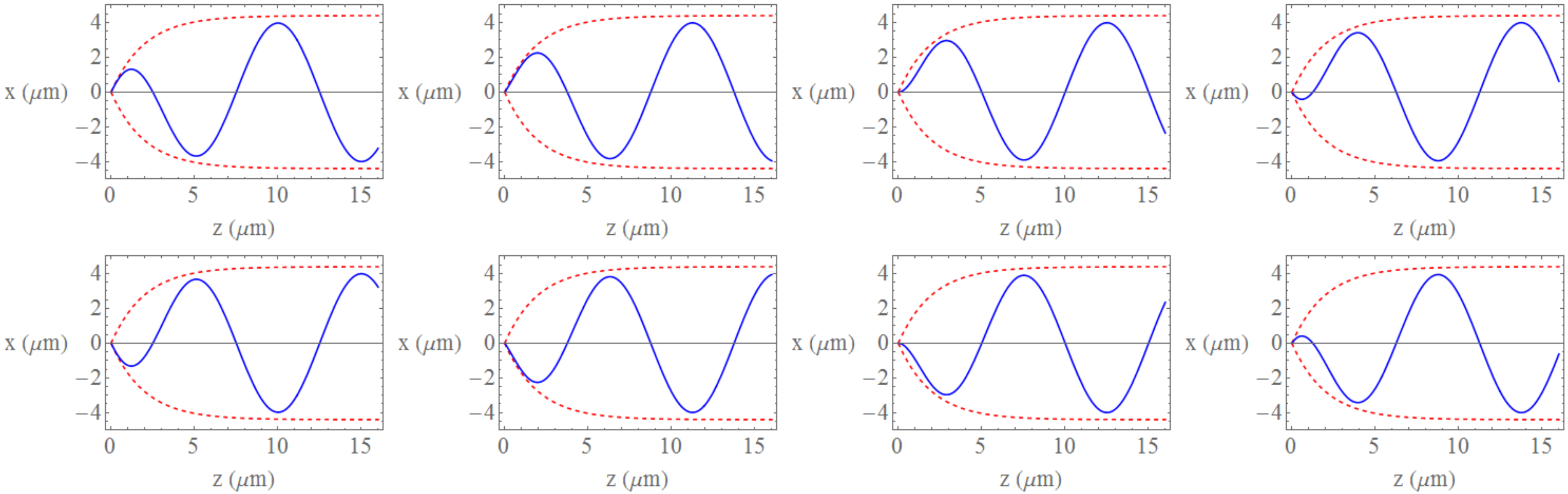
A & E: scale bar 5 µm



F: scale bar 1 µm

Mah, Christensen-Dalsgaard, and Leys, Evolution and Development **16**, 25-37 (2014).

Mulig pumpemekanisme



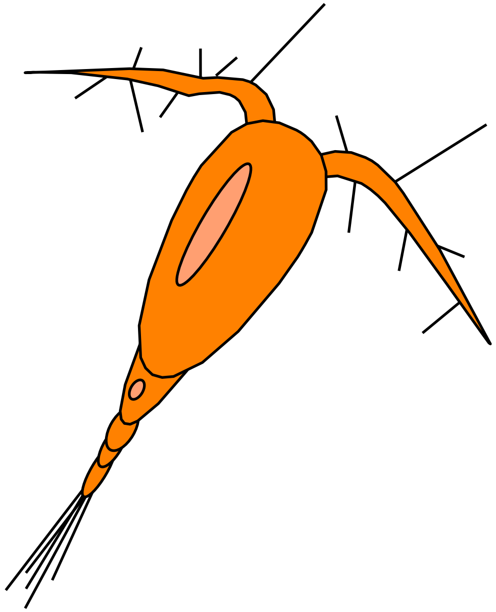
Beating flagellum with travelling wave that is moving away from the cell:

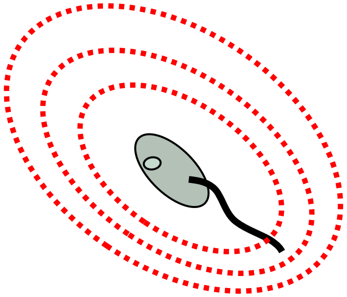
$$h(z,t) = A\left(1 - e^{-z/\delta}\right)\sin\left[2\pi\left(\frac{z}{\lambda} - \frac{t}{T}\right)\right]$$

Clearance rate estimate using pumping mechanism for flagellum with vane:

$$Q = \frac{\pi A^2 \lambda}{T} \approx 5 \cdot 10^3\,\mu\mathrm{m}^3\,\mathrm{s}^{-1}$$

III: Ambush feeding copepods

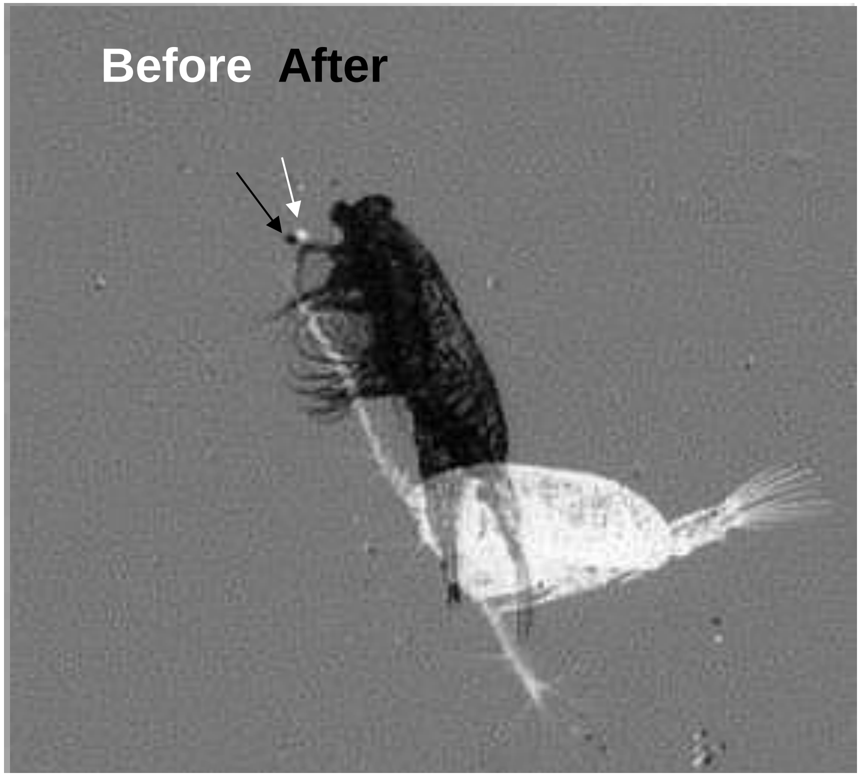


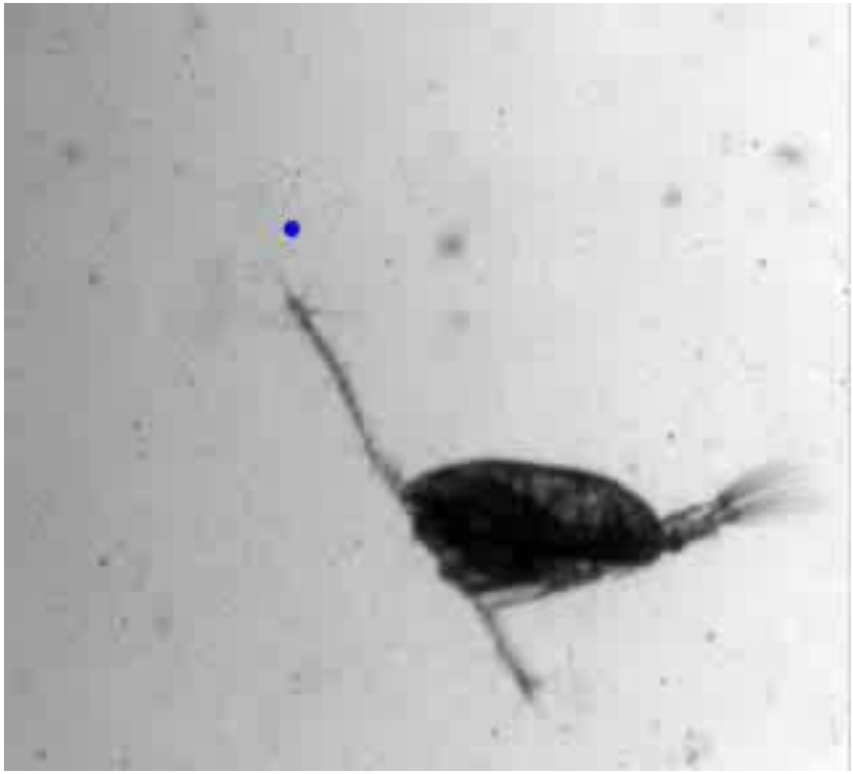


AMBUSH

SloMo: 1:5

SloMo: 1:270





Acartia tonsa

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

1 mm

Kiørboe et al. *PNAS* 2009

Boundary layer thickness

Scaling analysis

The viscous boundary layer grows as a diffusion prosses:

$$\delta \approx \sqrt{\nu t}$$

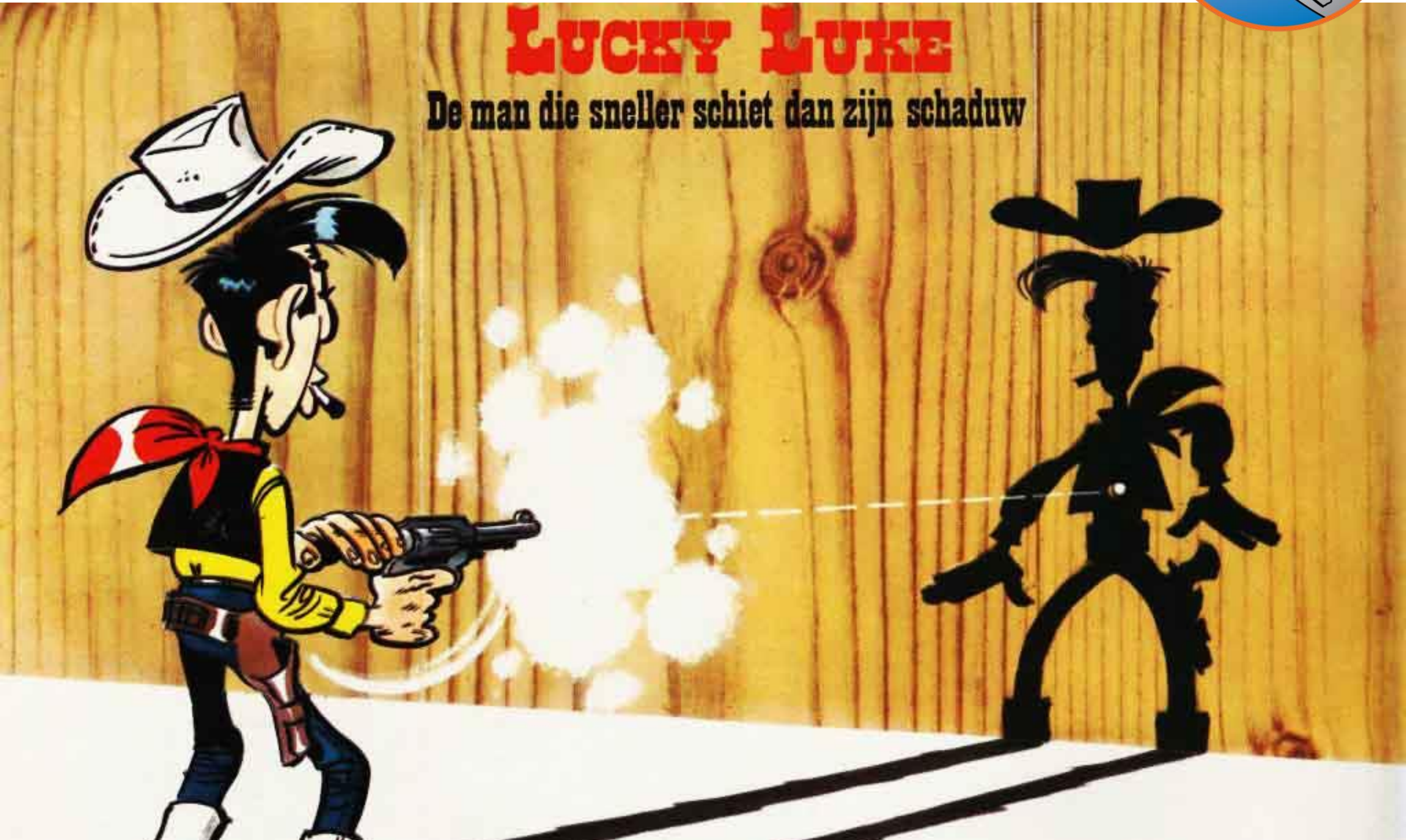
Relative thickness of viscous boundary layer at end of jump:

$$\frac{\delta}{L} \approx \sqrt{\frac{\nu T}{L^2}} \propto (LU_{\max})^{-0.5}$$

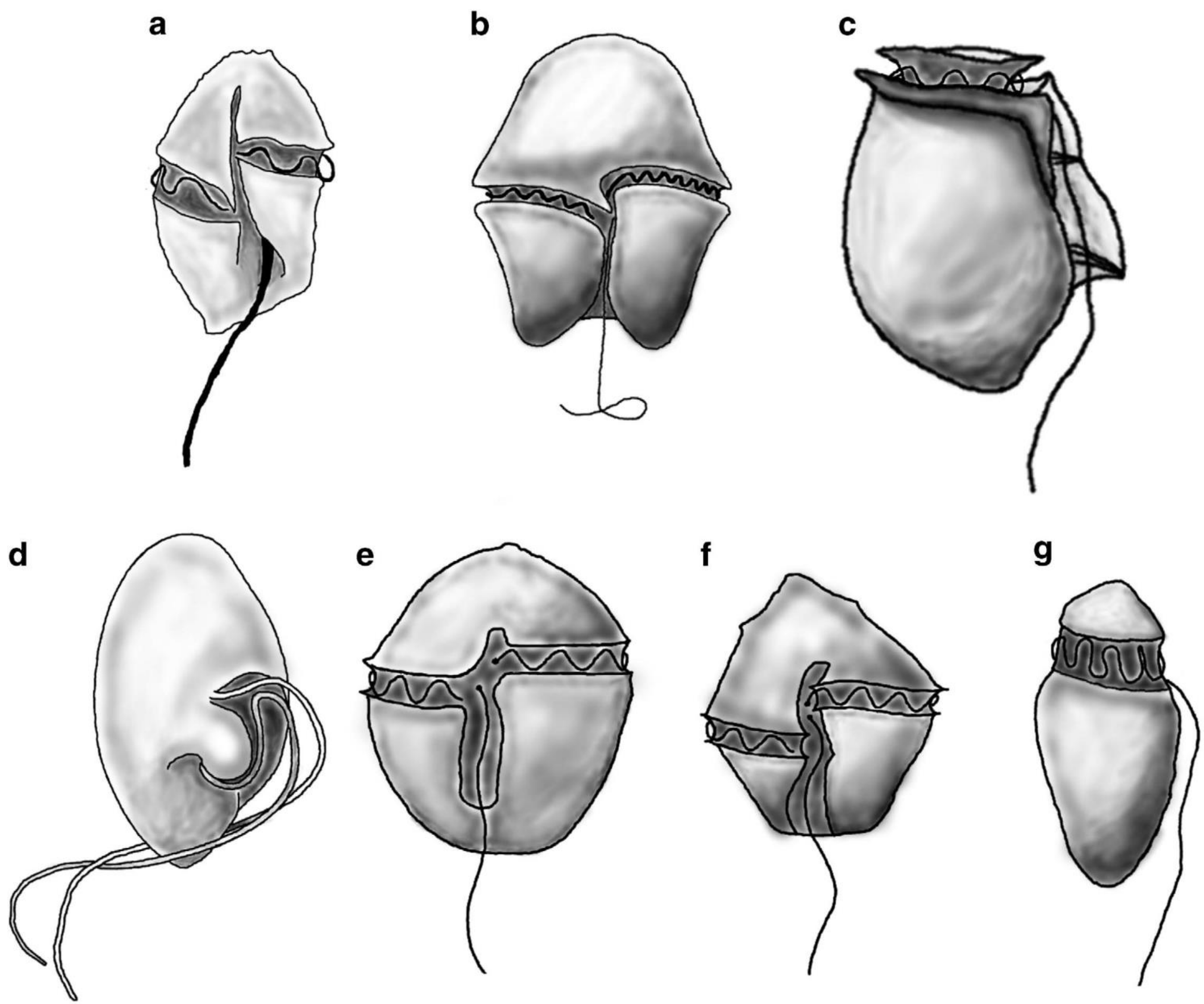
Assuming constant accelleration during time *T* and jump of one body length *L*

SPEED IS KEY TO SUCCES!

Lucky Luke princippet



IV. How dinoflagellates feed and swim



The boundary layer problem

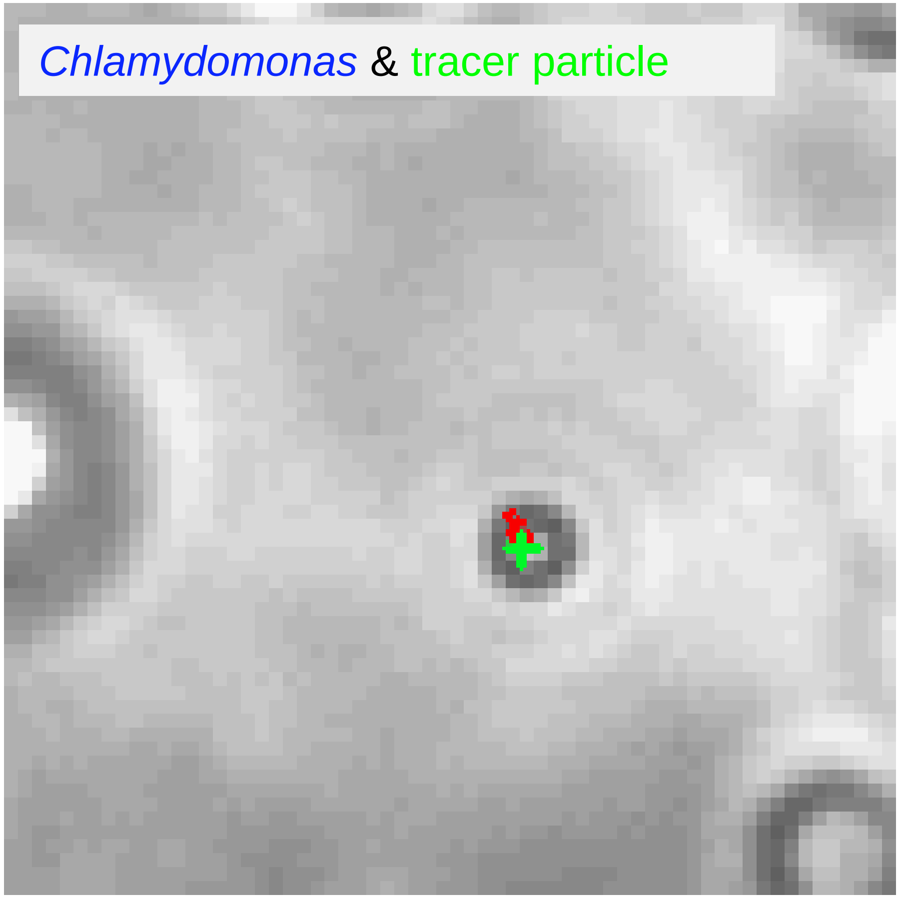
The boundary layer problem

Size: 1-100 µm

Low Reynolds number =
high viscosity

Thick viscous boundary layer will
push prey away

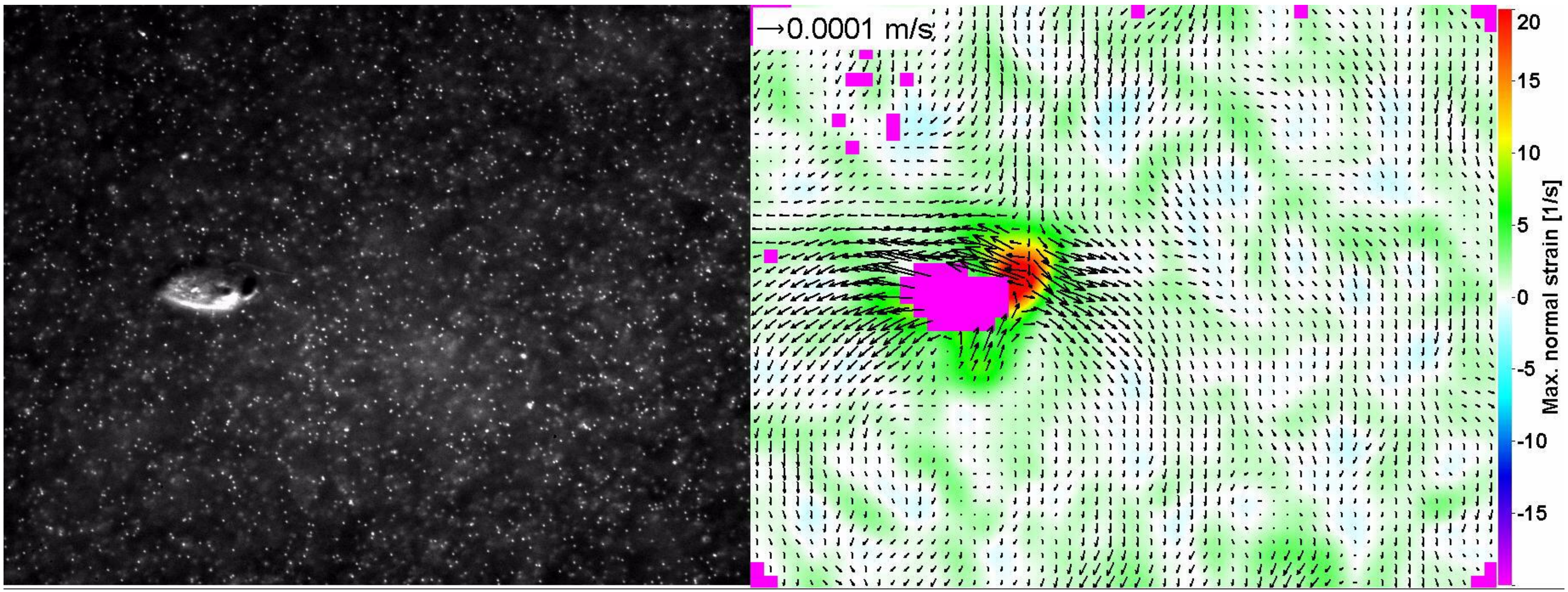
Speed is NOT the solution

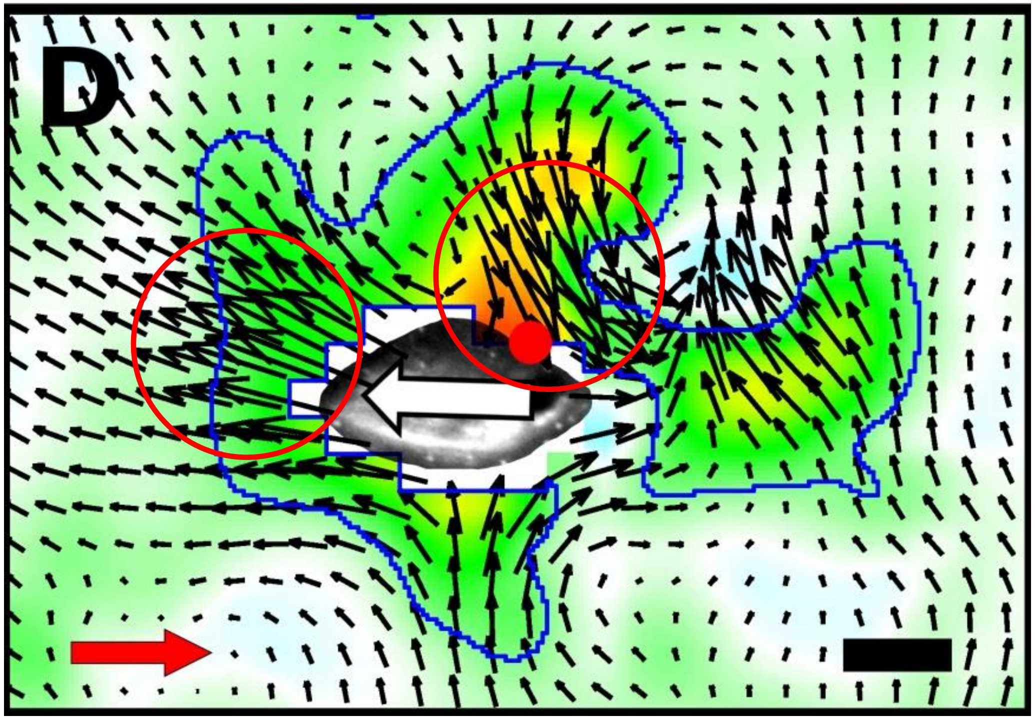


Goldstein video

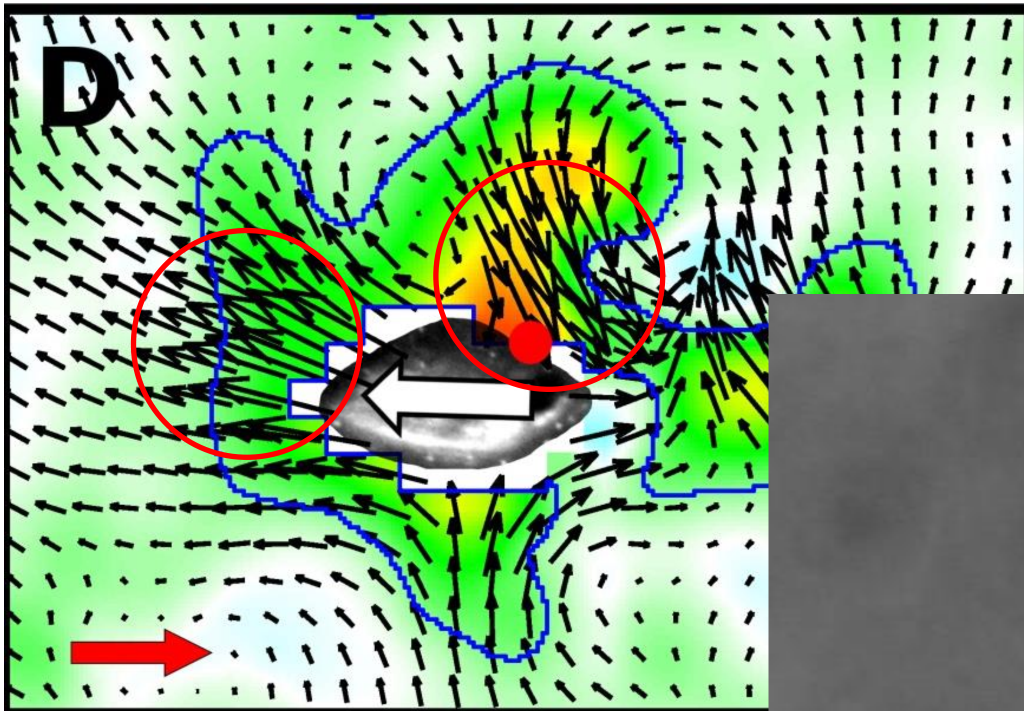
Flow field

Oxyrrhis marina





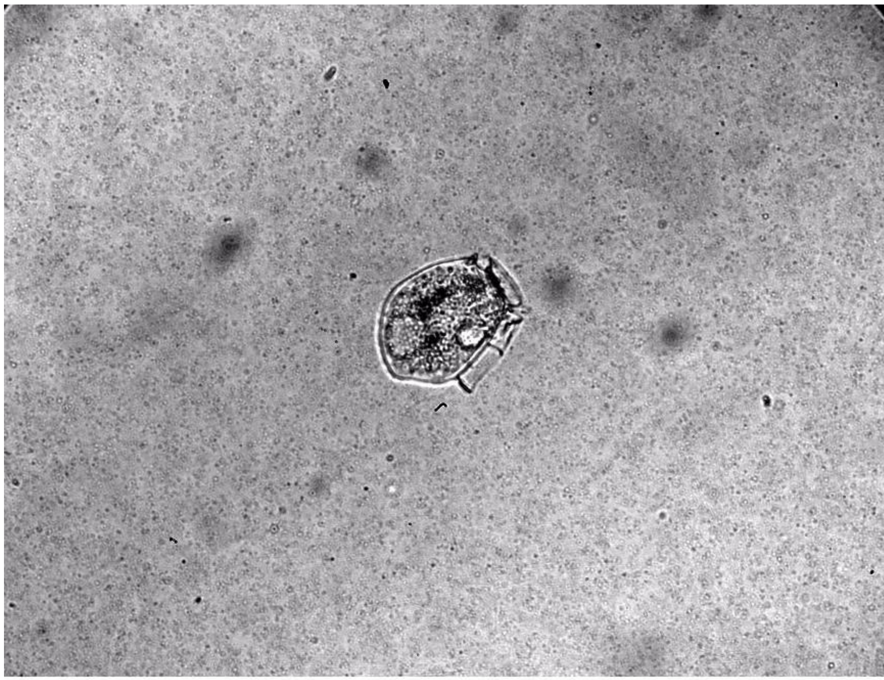
- Push water in front of the cell
- Feeding current towards point of prey capture

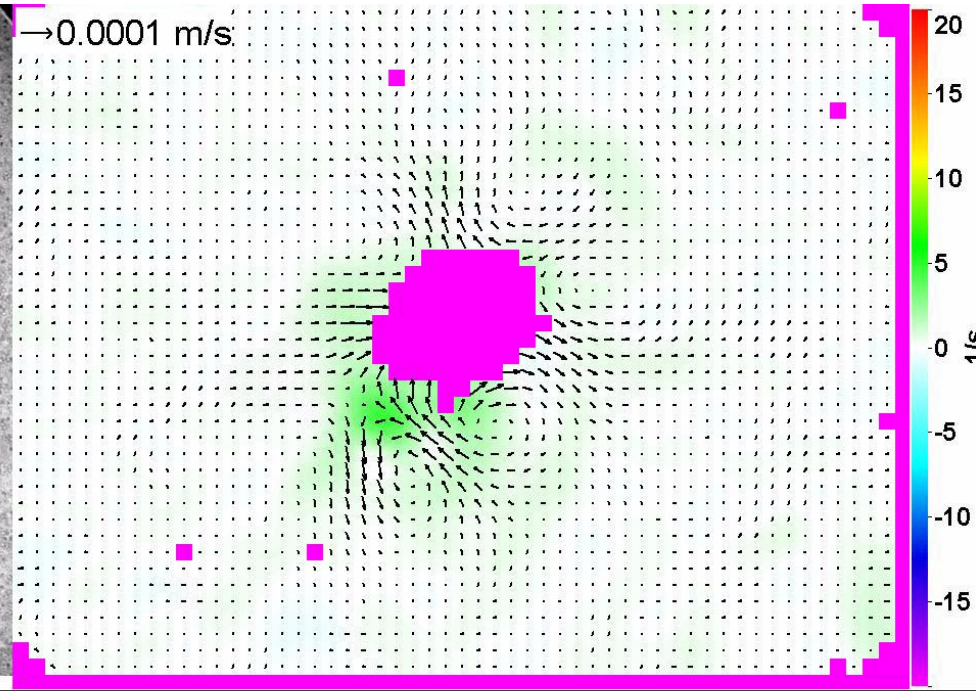


- Push water in front of the cell
- Feeding current towards point of prey capture

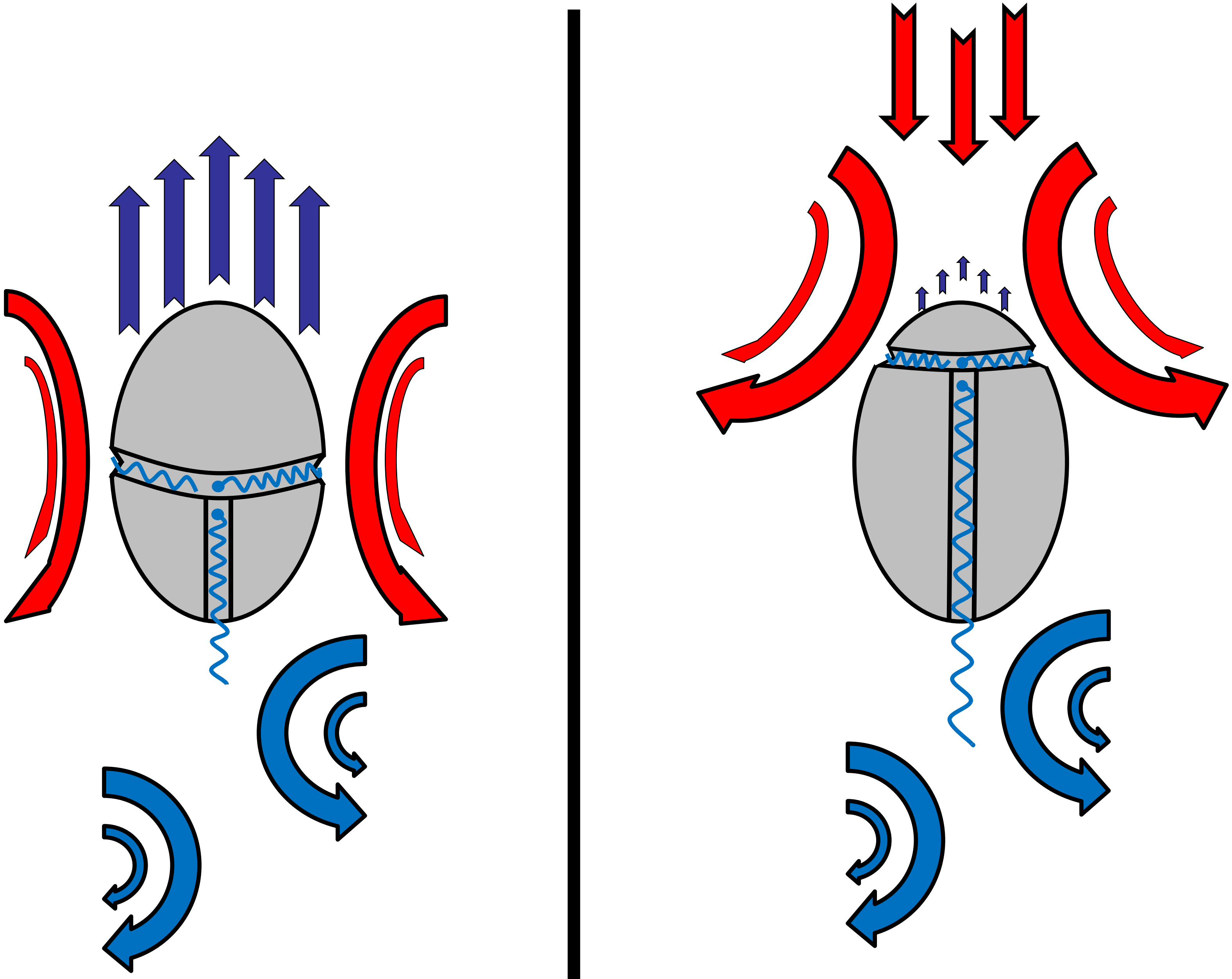
Dinophysis

Tværflagellen monteret frontalt





Mesodinium
SloMo 1:1000

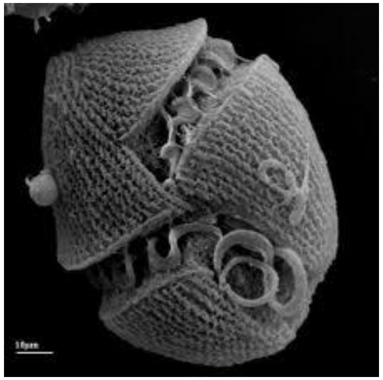


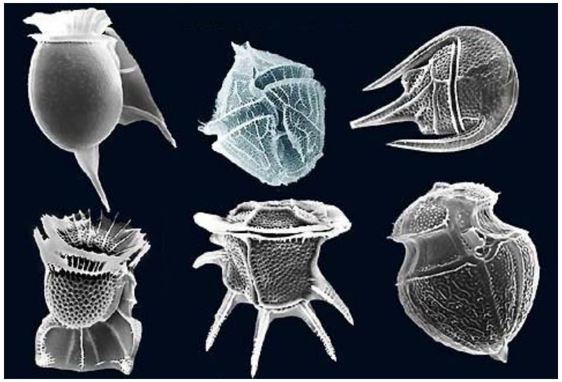
How are propulsion and feeding current generated?

No consensus

Lindemann, 1928: Dinoflagellates continue to move forward after losing the longitudinal flagellum ➔ Transverse flagellum must provide the majority of the thrust

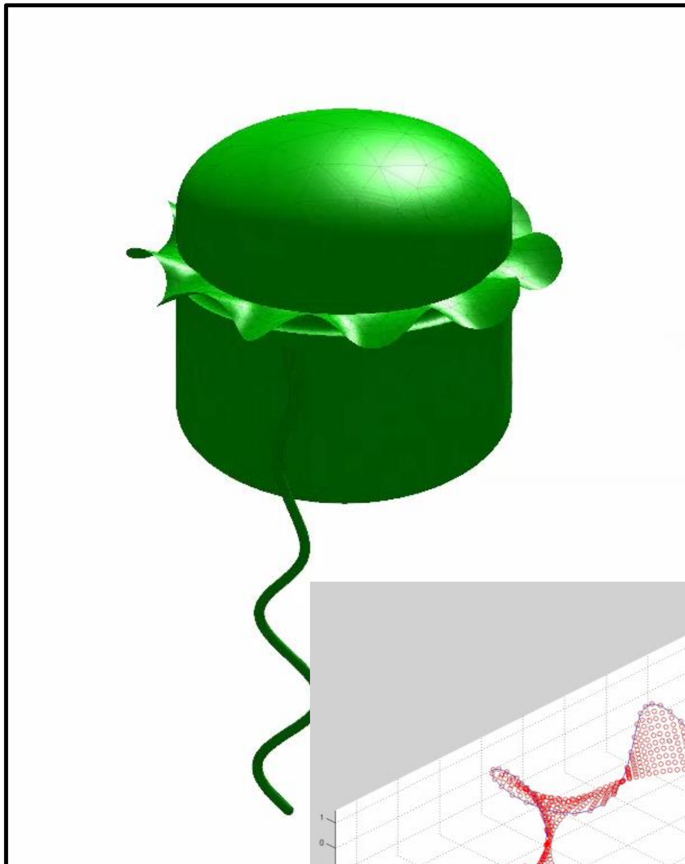
Fenchel, 2001: The longitudinal flagellum provides the forward thrust; the transverse flagellum rotates the cell. Together, the rotational forces allows steering.

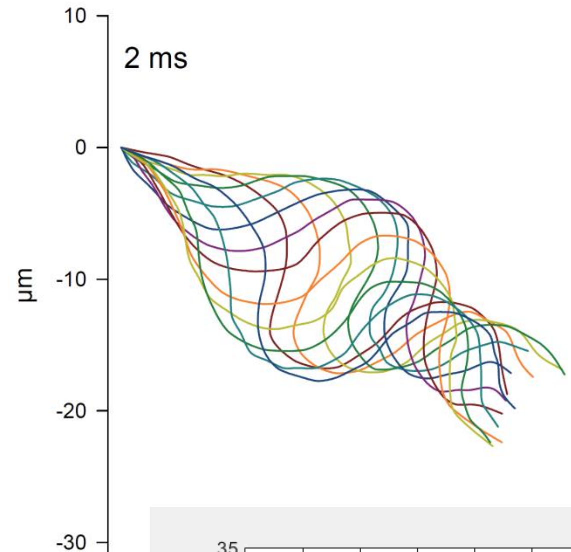


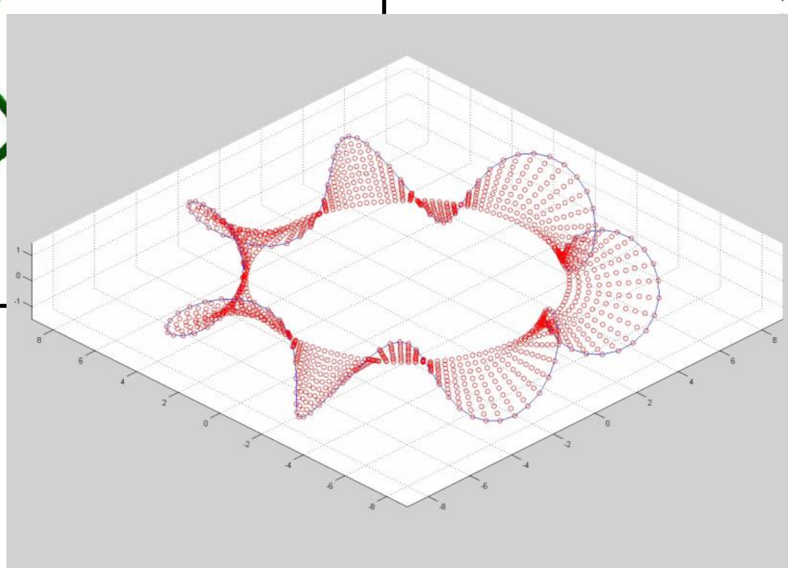


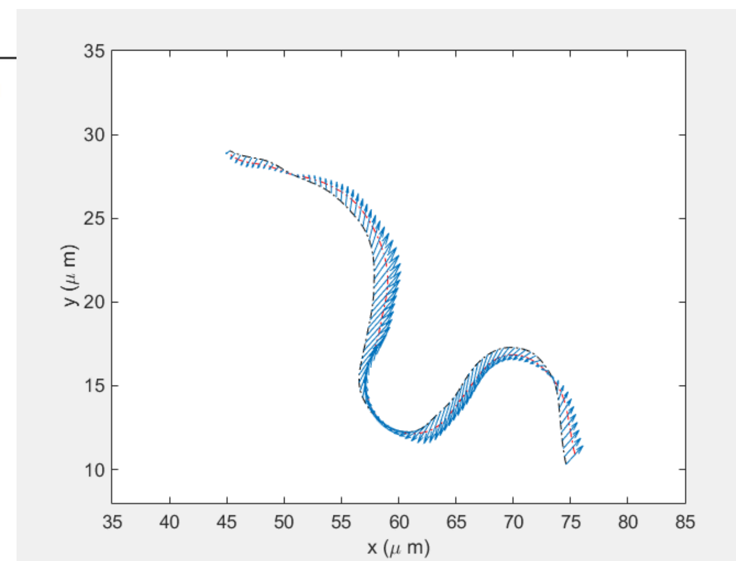
Build a model

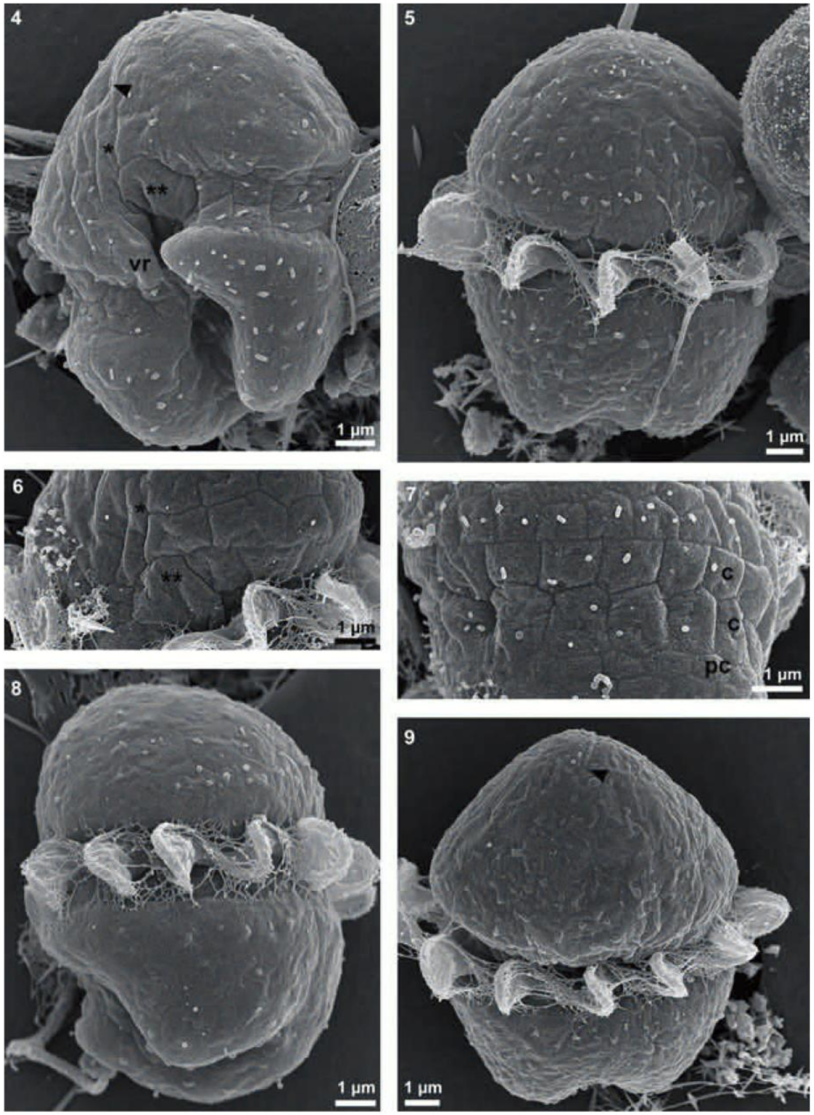
Components: transverse flagellum, longitudinal flagellum, cell body











Figs 4–9. Scanning electron microscopy of *Biecheleriopsis adriatica* gen. et sp. nov. 4. Slightly oblique ventral view showing asymmetry of the cell and the ventral termination of the elongate apical vesicle (EAV). The deep antapical excavation is seen ir in Figures 5 and 9. The sulcus remains deeply invaginated until reaching the epicone where it terminates in a single large vesicle (two asterisks, Fig. 4), also visible in another cell in Figure 6. Figure 5 is a dorsal view of a cell with a rounded epic the conspicuous transverse flagellum (see also Figs 8,9). 7. The two horizontal rows of cingular vesicles; the upper pentagonal and the lower are hexagonal. The vesicles in the postcingular row are significantly smaller than other vesicles. 8. Left lateral view showing the shorter and more dorso-ventrally compressed left side of the hypocone. 9. Upper of cell with cone-shaped epicone showing the dorsal extension of the EAV. Arrowheads mark the EAV. c, cingular plates; pc, plates; vr, ventral ridge area. The large vesicle at the upper end of the sulcus has been marked by two asterisks, while the sir marks the adjacent elongate vesicle that almost reaches the EAV (see also Figs 10–13).

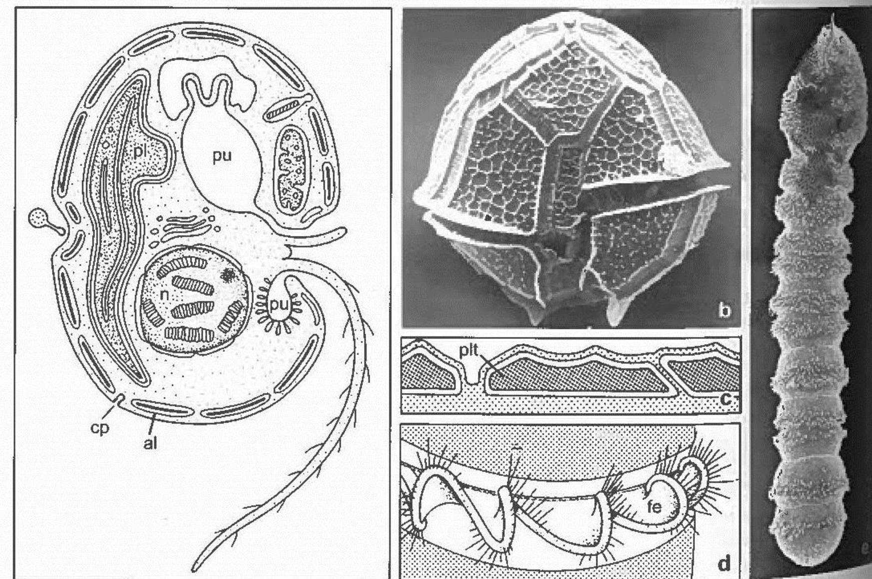
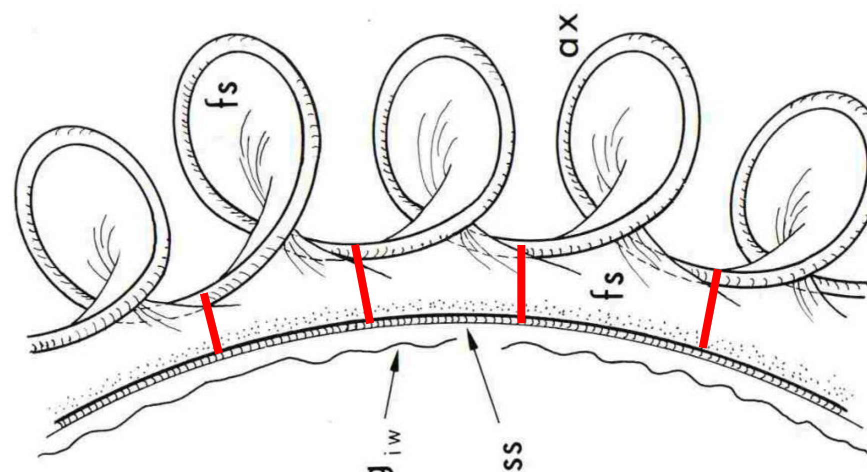
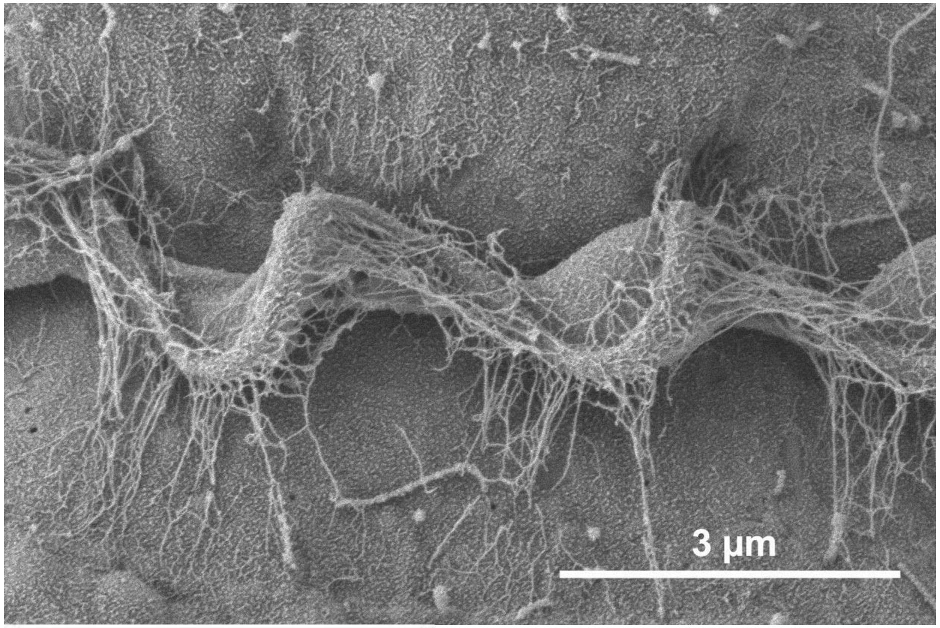


Fig. 80 Alveolata, Dinoflagellata: **a** scheme of internal organization; **b** thecal plates of *Peridinium bipes*; **c** amphiesmal vesicles with cellulose plates (plt); **d** cingulum flagellum with mastigonemes and flagellar extension (fe = paraxial hem); **e** chain formation in the parasitic *Haplozoon axiothellae*. cp = collared pit, n = nucleus, pl = plastid, plt = amphiesmal plate, pu = pusule, tr = trichocyst (a after Taylor; b courtesy of R. M. Crawford, Bristol; c and d after Gaines and Taylor; e from Leander et al.: Europ. J. Protistol. 38 [2002] 287). Magn.: b 1,000 ×, e 800 ×.



Berdach 1977

()


3 µm

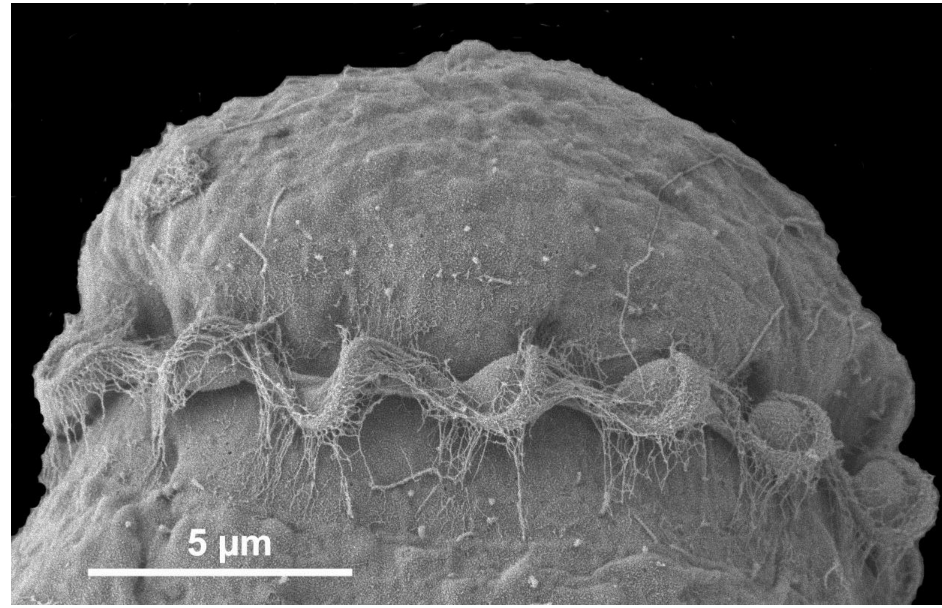
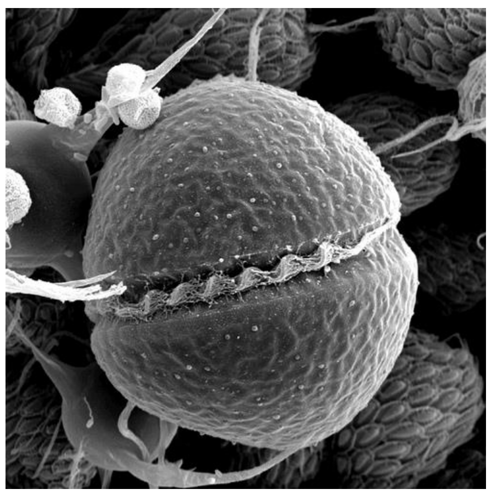
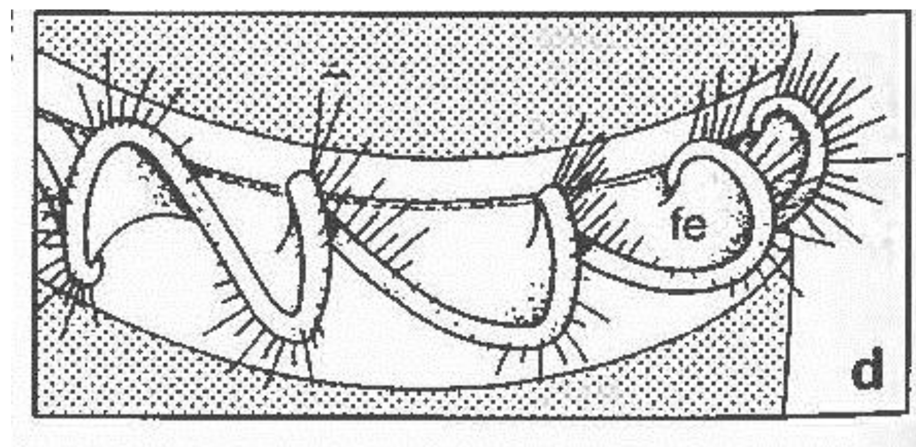

5 µm


Photo:Gert Hansen



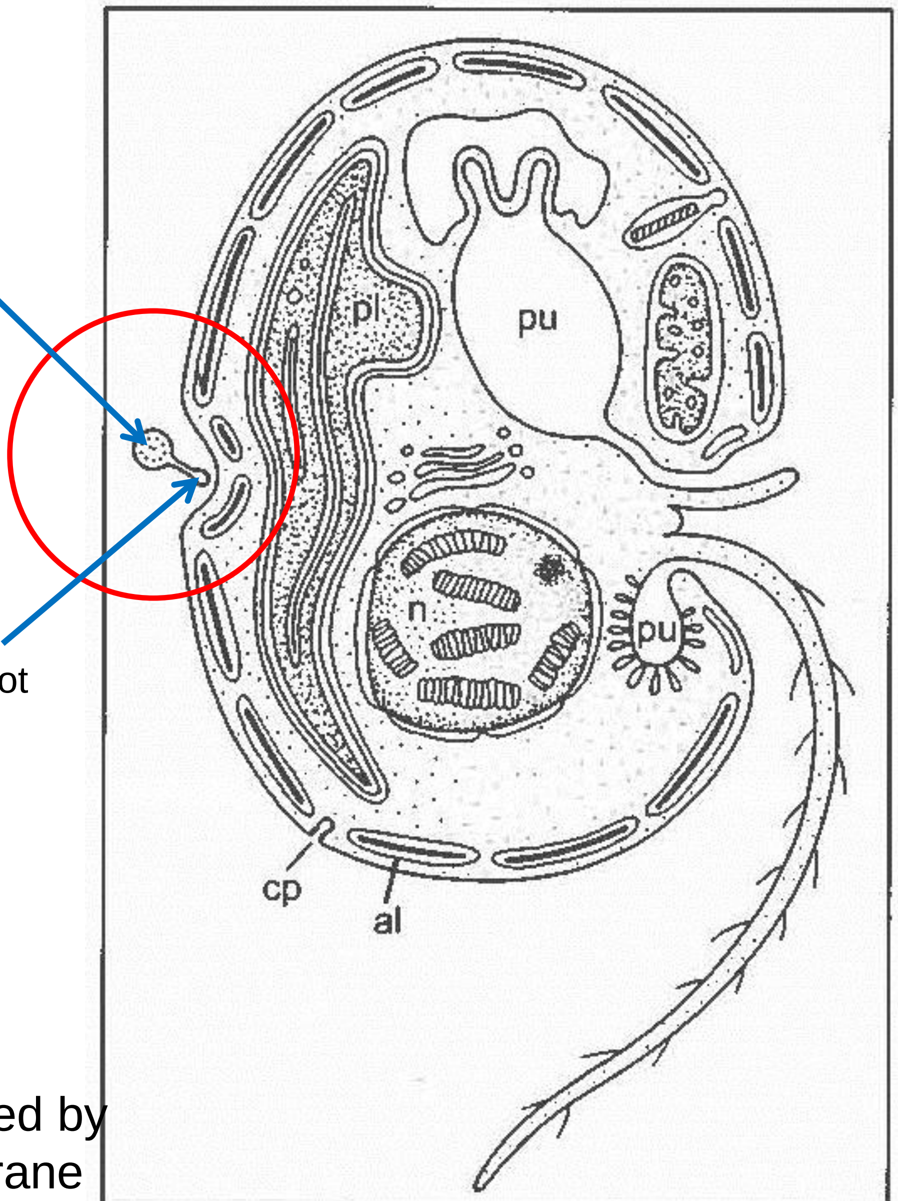

fe
d

‘Axoneme’

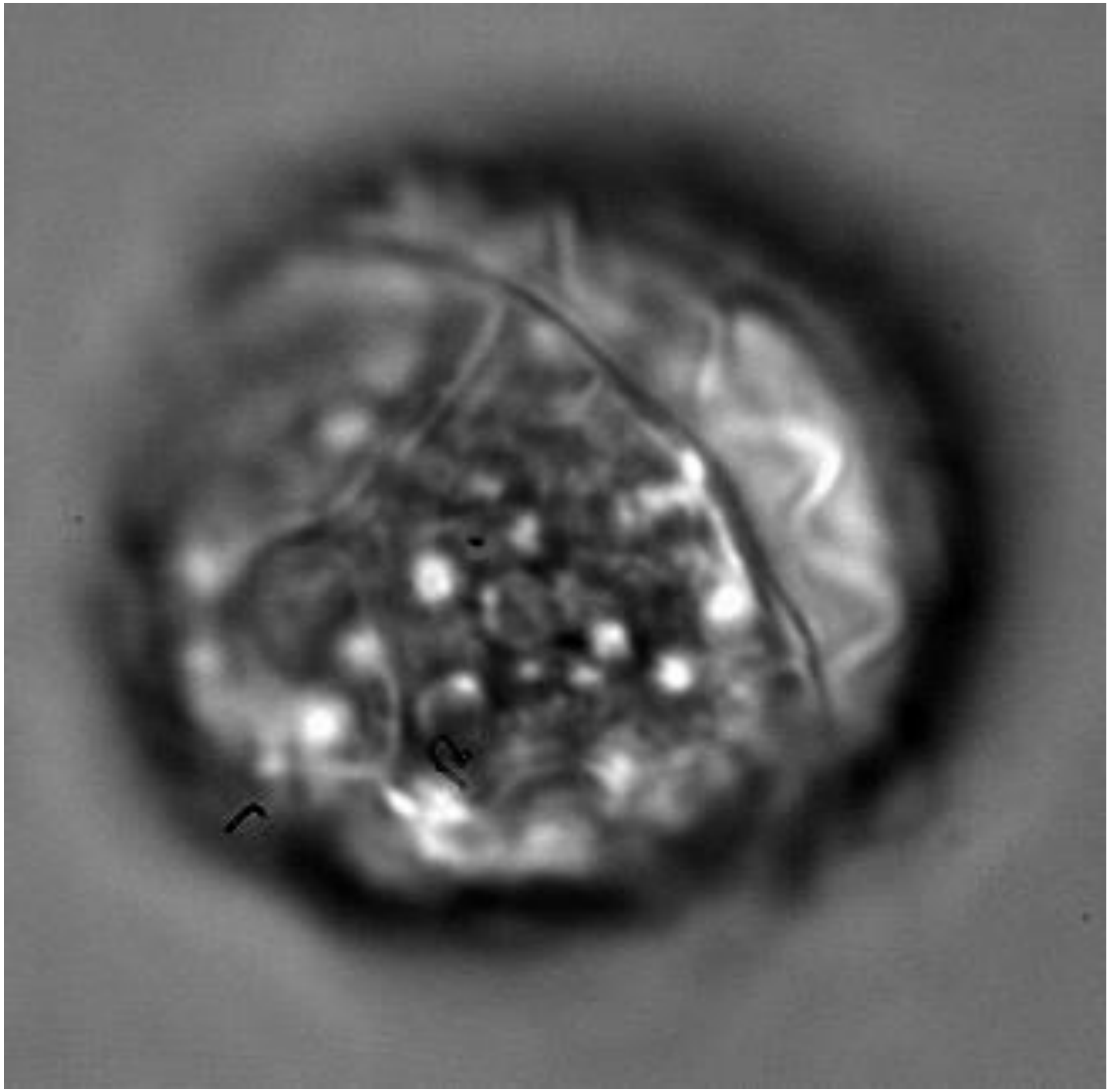
The part we perceive as the flagellum. Moves up/down in a 2/3D motion.

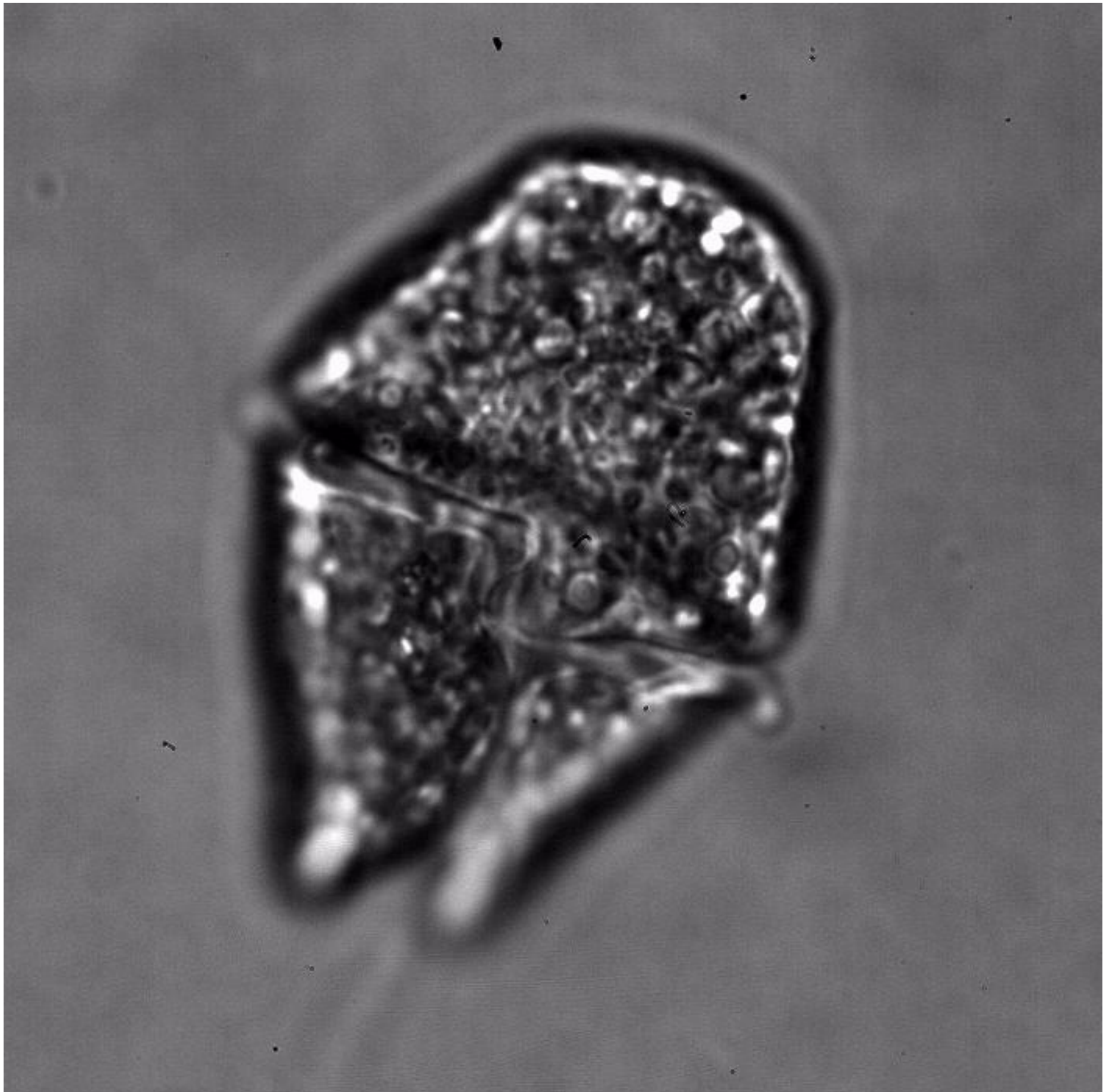
‘Paraxial rod’

Stiff rod. Supposedly not moving.

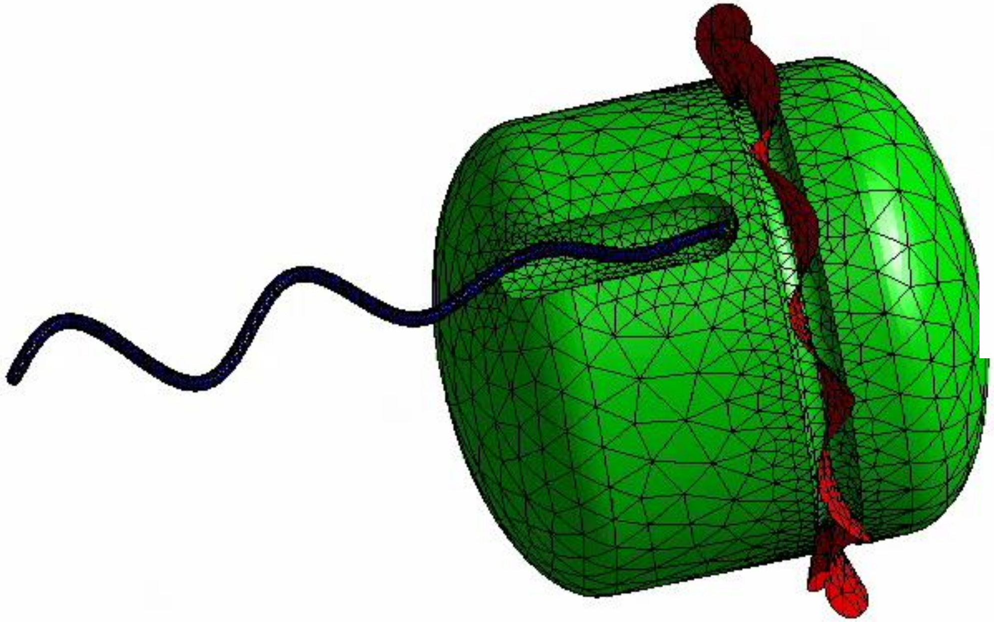


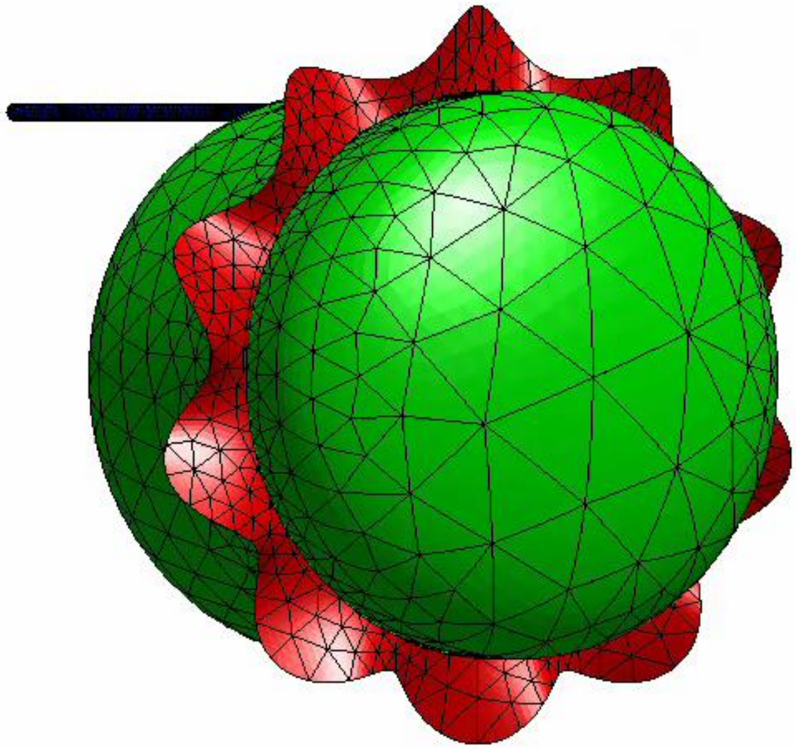
Both part enclosed by the same membrane ‘sock’





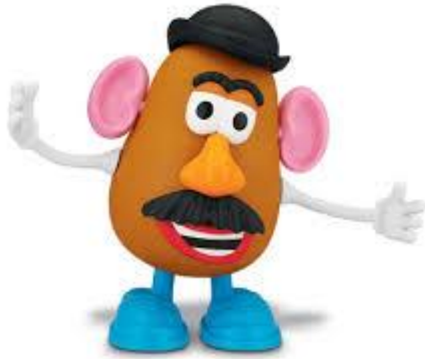
Maskineriet spiller

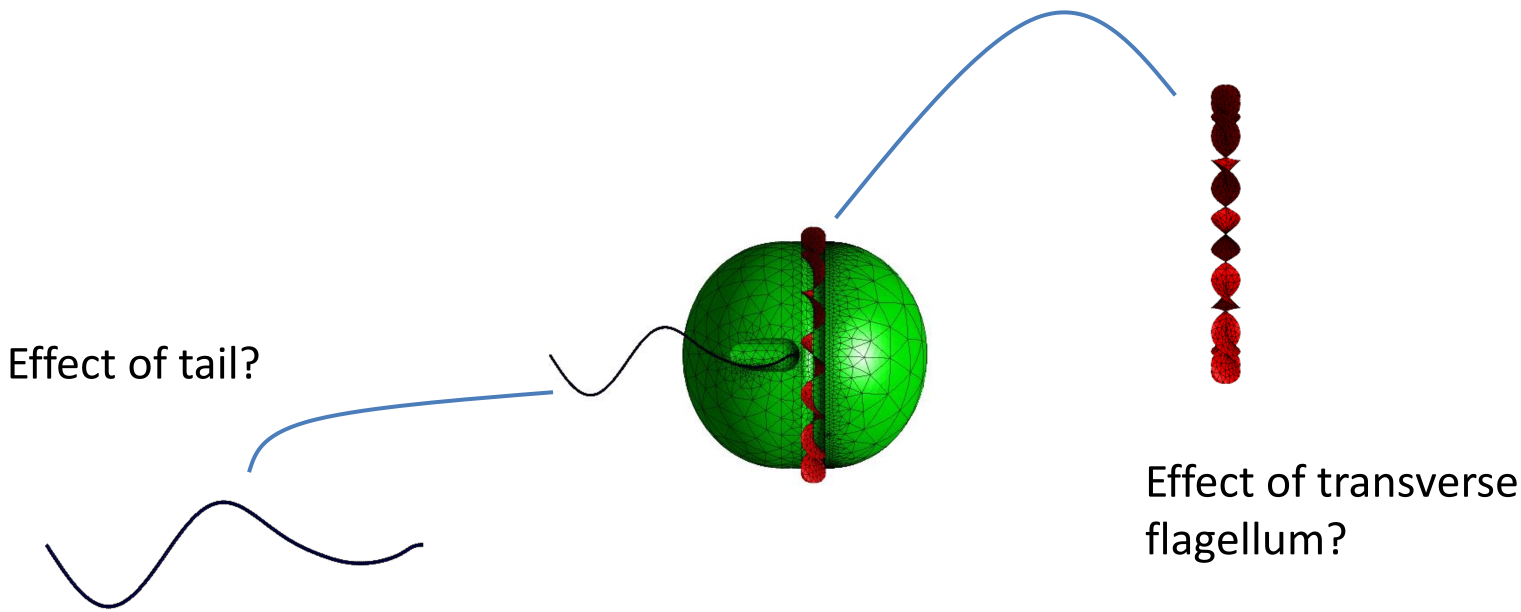




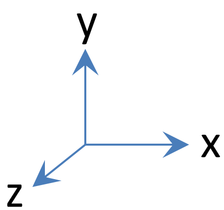
Vi kan bergegne den resulterende fødestrøm (in progress) og sammenligne med det observerede

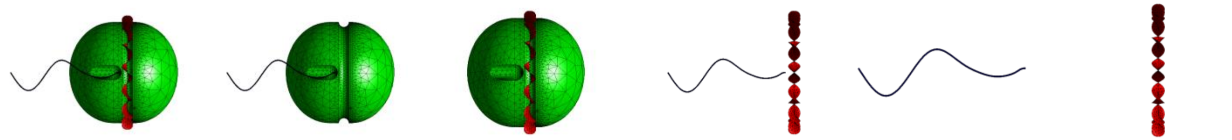
Vi kan eksperimentere med modellen





Preliminary Results: swimming kinematics at one instant in time

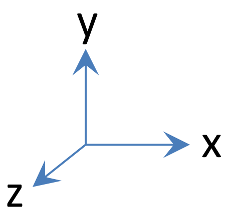


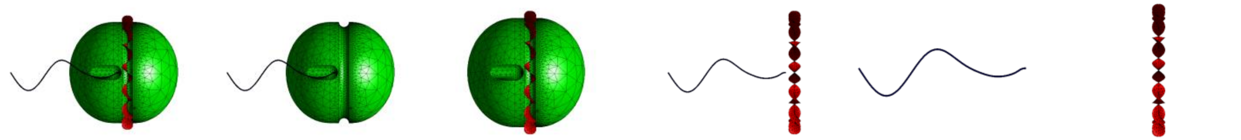


µm / s		**Body Tail Transverse**	Body Tail	Body Transverse	Tail Transverse	Tail	Transverse
	x - velocity	**55.7**	12.5	45.1	130.0	187.6	117.3
	y - velocity	**4.8**	9.3	-0.9	-4.4	-164.0	-0.3
	z - velocity	**5.8**	8.4	-0.2	0.3	-0.9	0.3

deg / s		**Body Tail Transverse**	Body Tail	Body Transverse	Tail Transverse	Tail	Transverse
	x - rotation	**-110.1**	4.5	-121.8	-182.6	11.0	-233.7
	y - rotation	**39.3**	50.2	1.3	33.8	5.2	-0.2
	z - rotation	**-49.8**	-57.6	-4.0	-57.6	-790.1	0.3

Preliminary Results: turn hydrodynamic interactions OFF



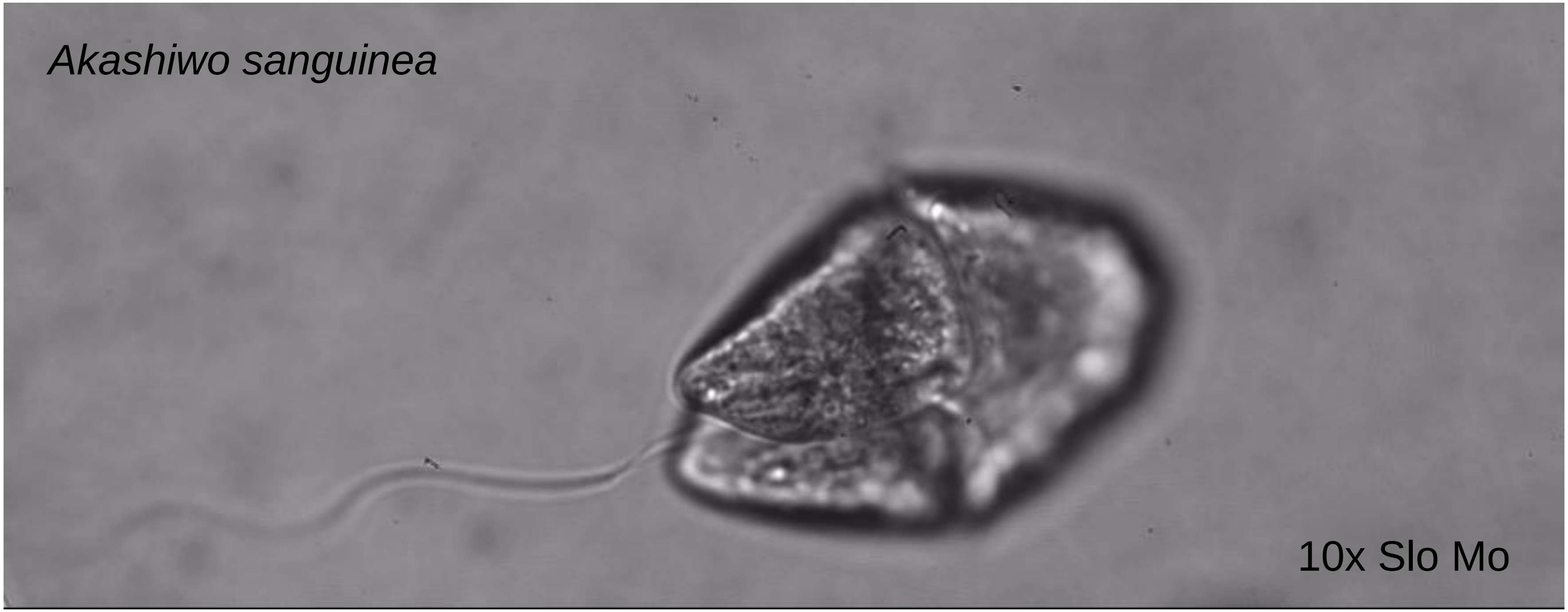


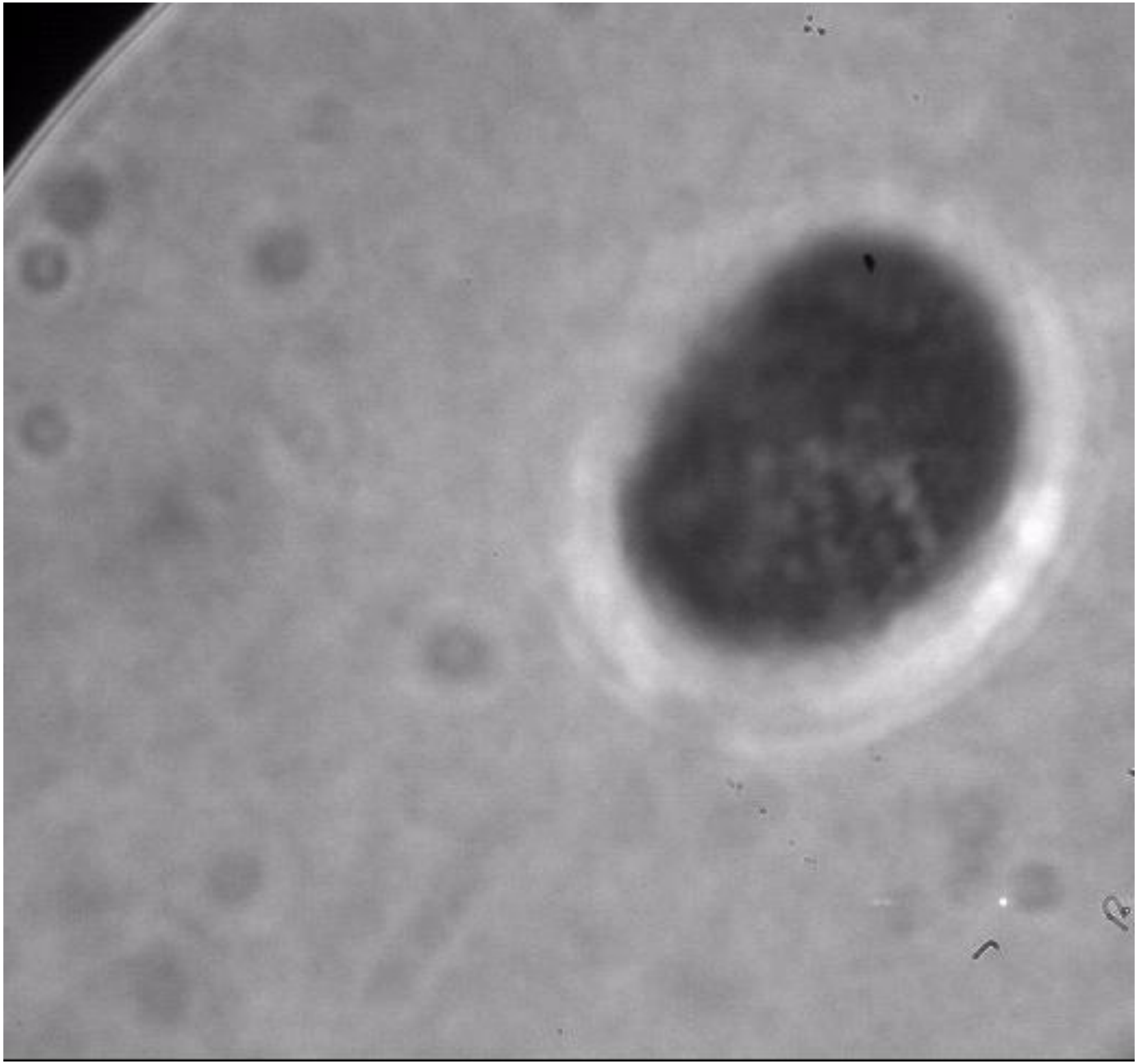
		Body Tail Transverse	Body Tail	Body Transverse	Tail Transverse	Tail	Transverse
µm / s	x - velocity	**64.2**	28.1	51.6	129.8	187.6	117.3
	y - velocity	**-0.2**	3.9	-0.2	-11.6	-164.0	-0.3
	z - velocity	**2.2**	2.4	0.2	0.7	-0.9	0.3

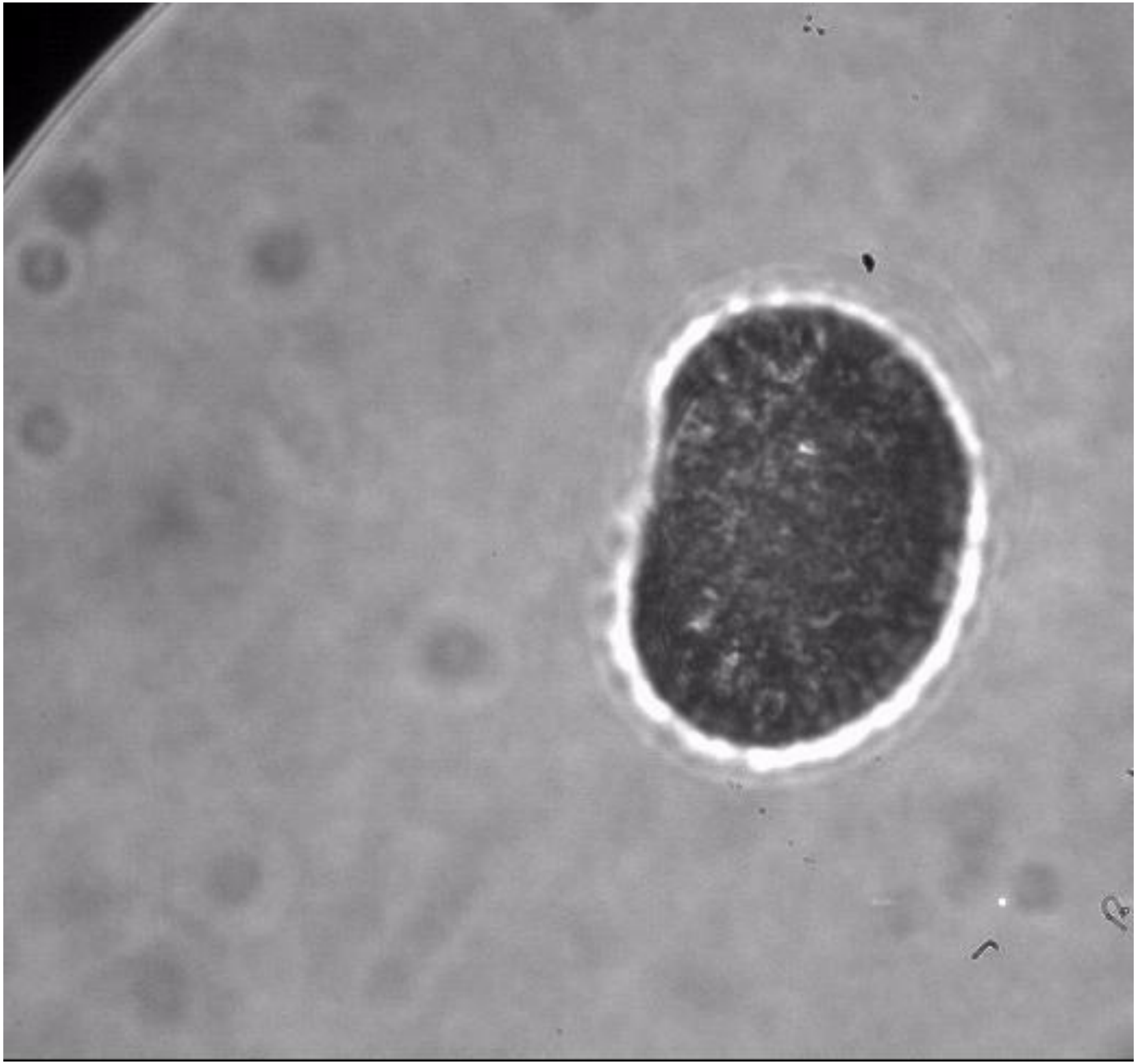
deg / s	x - rotation	**-80.3**	8.2	-92.1	-178.7	11.0	-233.7
	y - rotation	**25.5**	45.0	0.1	22.5	5.2	-0.2
	z - rotation	**-32.8**	-54.6	0.0	-67.1	-790.1	0.3

Mysteriet

Sammenlign cellens rotation og tværflagellens slagretning



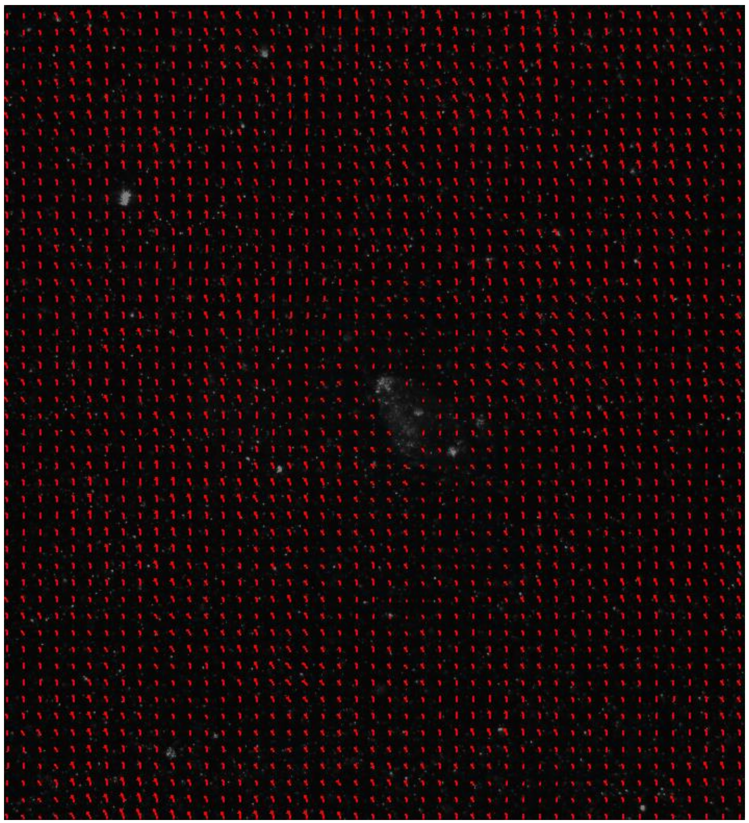




V. Hvordan gemmer plankton sig?

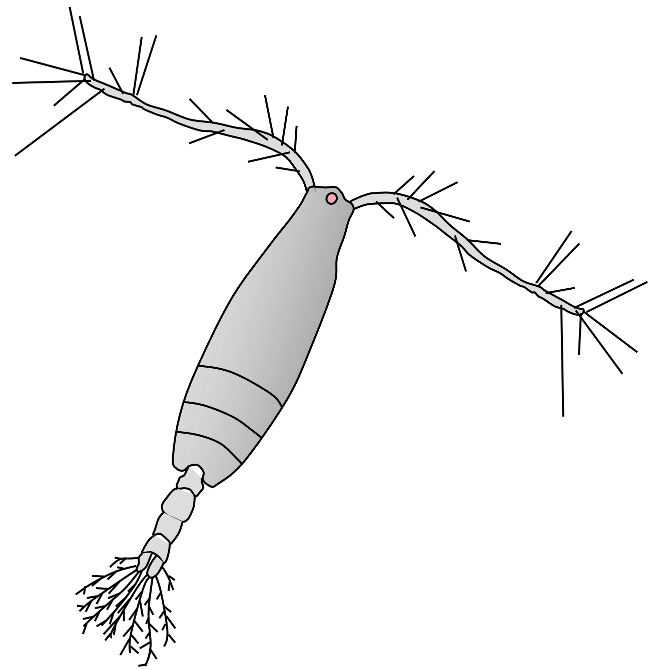
Enhver aktivitet giver anledning til hydrodynamisk støj

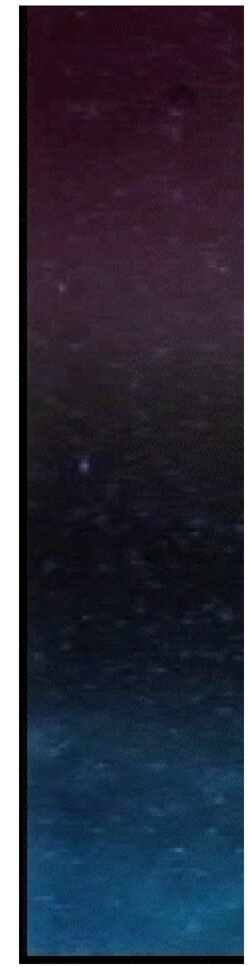
SloMo 1:200



0.3 mm

N. Wadhwa





J. Strickler

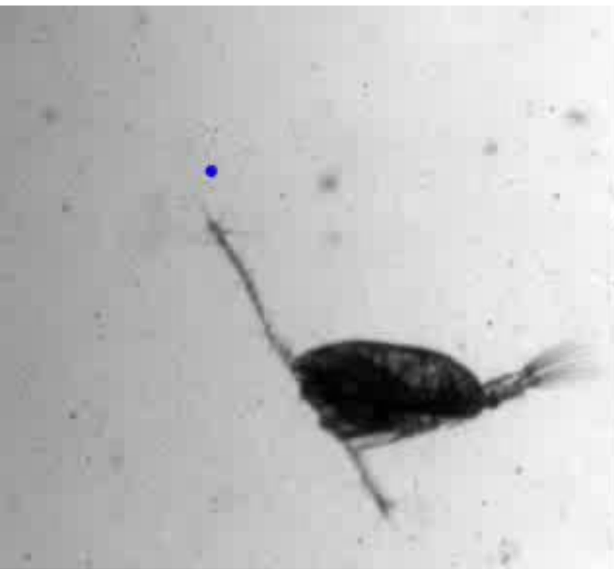
Hvordan gemmer plankton sig?

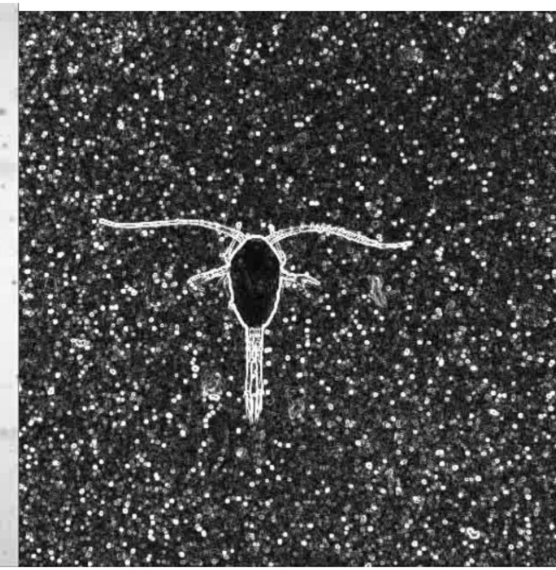
Tre principielt forskellige måder at æde på

Ambush

Cruise

Feeding current (Hovering)





Passive feeding modes

Active feeding modes

All movies in SloMo
1:100-1:300

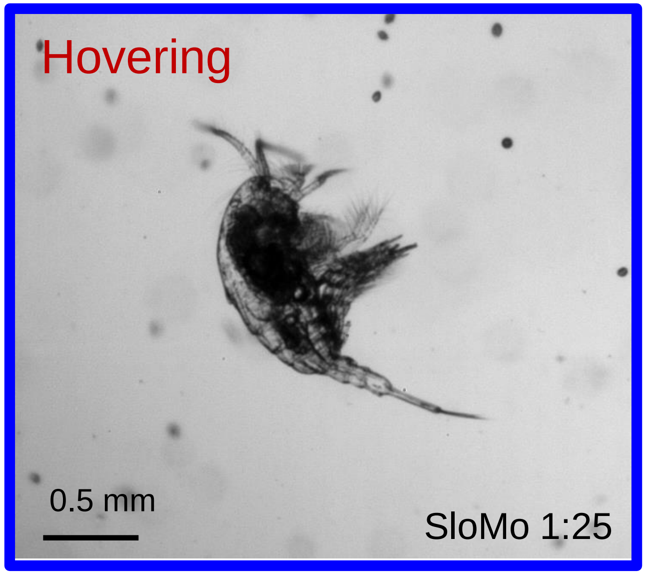
Kiørboe *Biol Rev* 2011

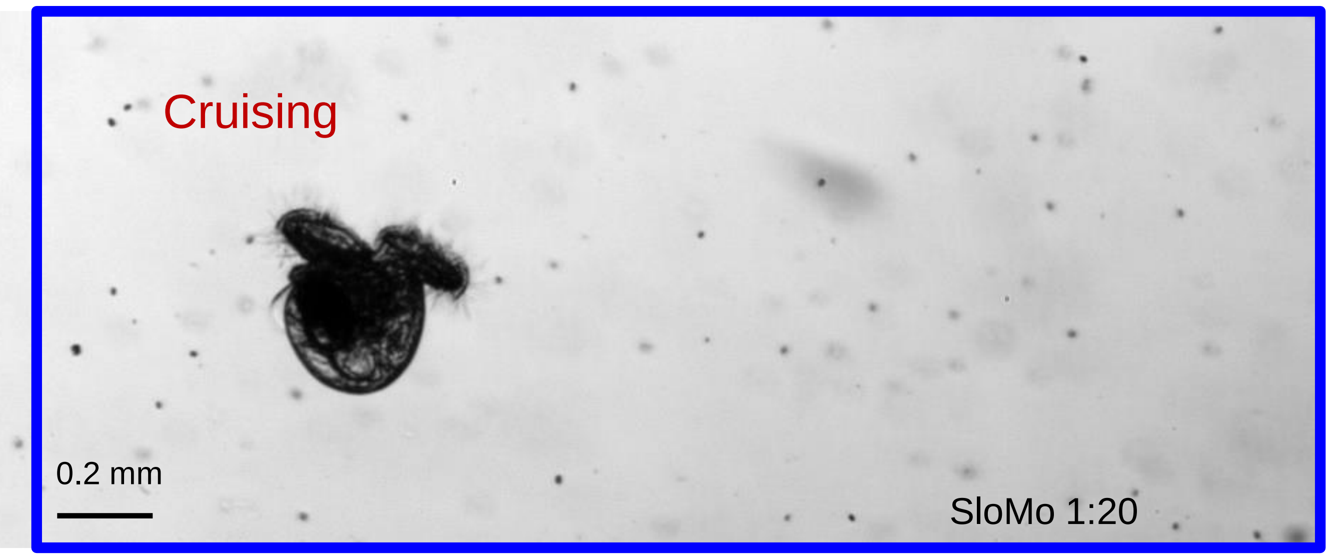
Four propulsion modes

Propulsion and feeding are partly related

Feeding and swimming
(active feeders)

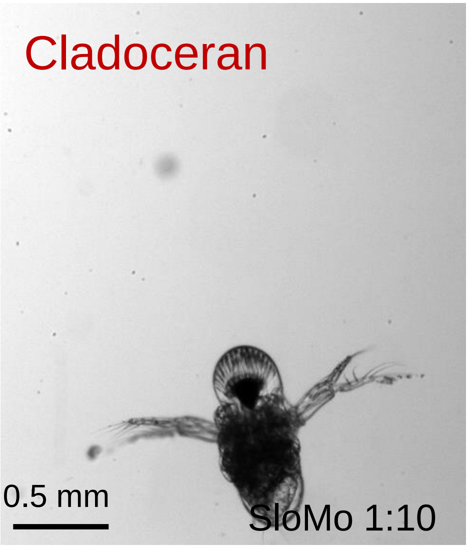
Swimming
(ambush feeders)

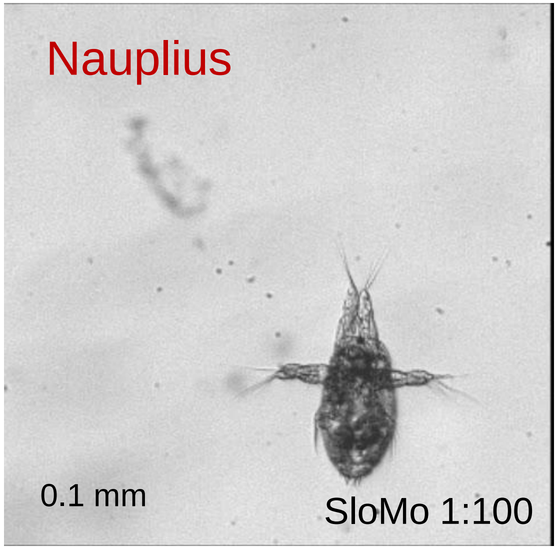


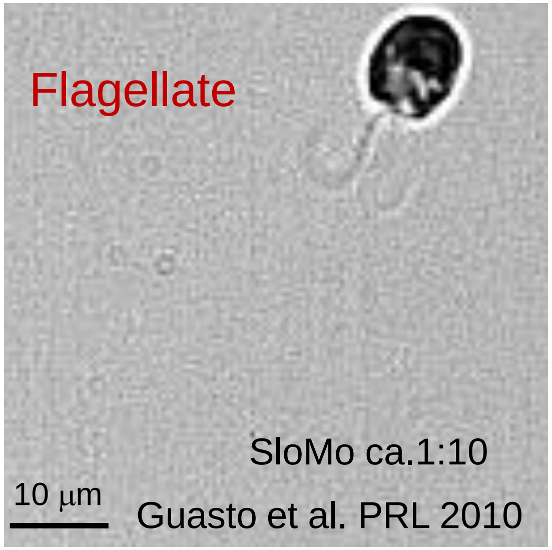


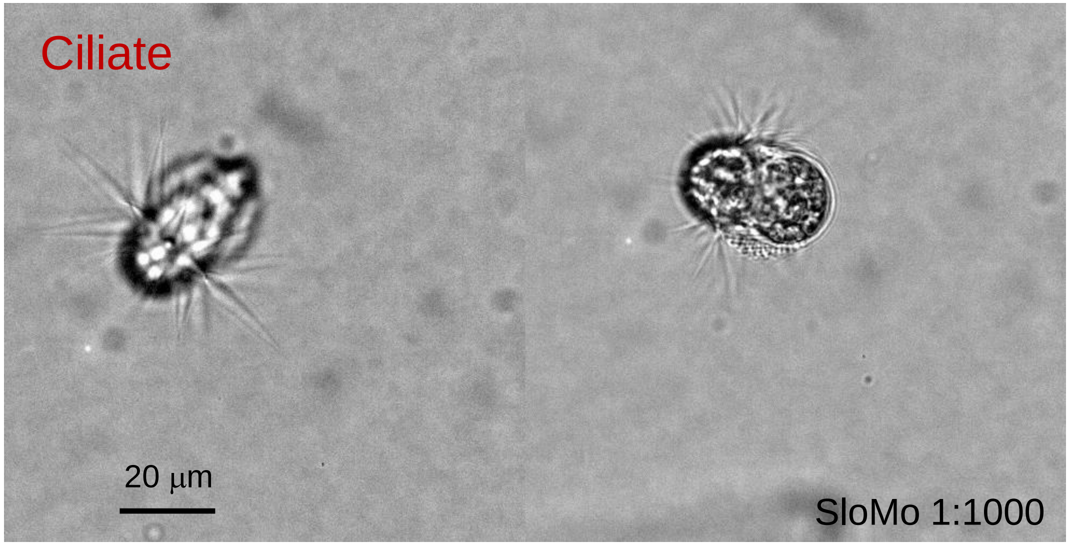
Diversity of breast strokers: Taxa transcending

Diverse organisms and diverse machineries



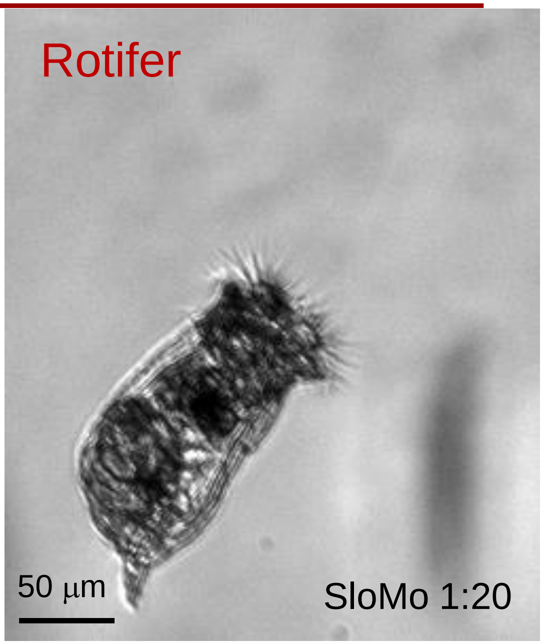


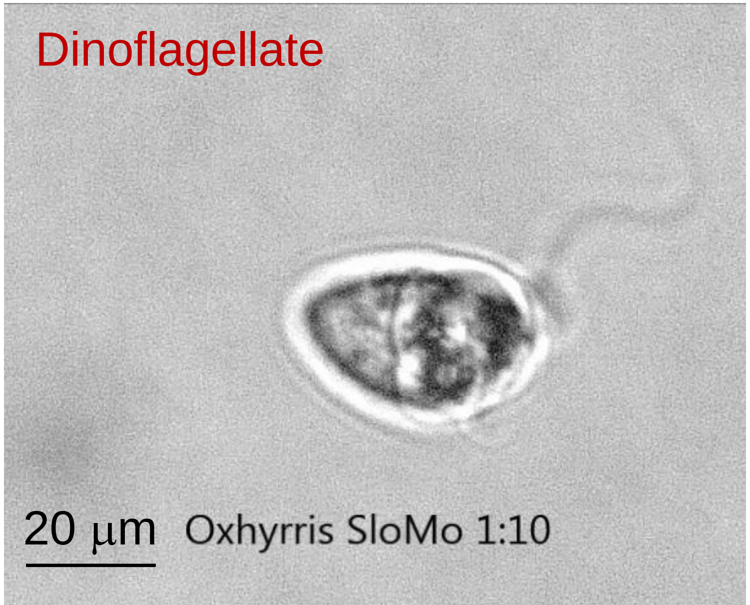


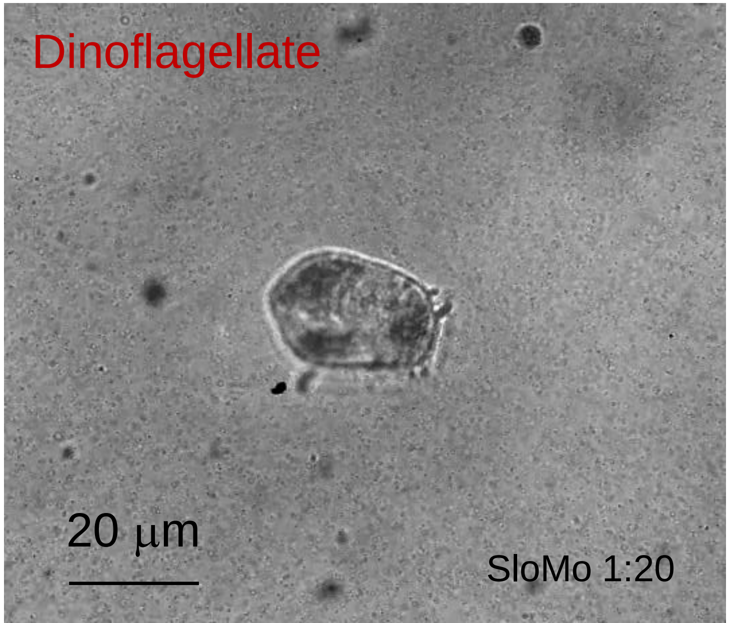


Diversity of cruisers: Taxa transcending

Pushers and pullers

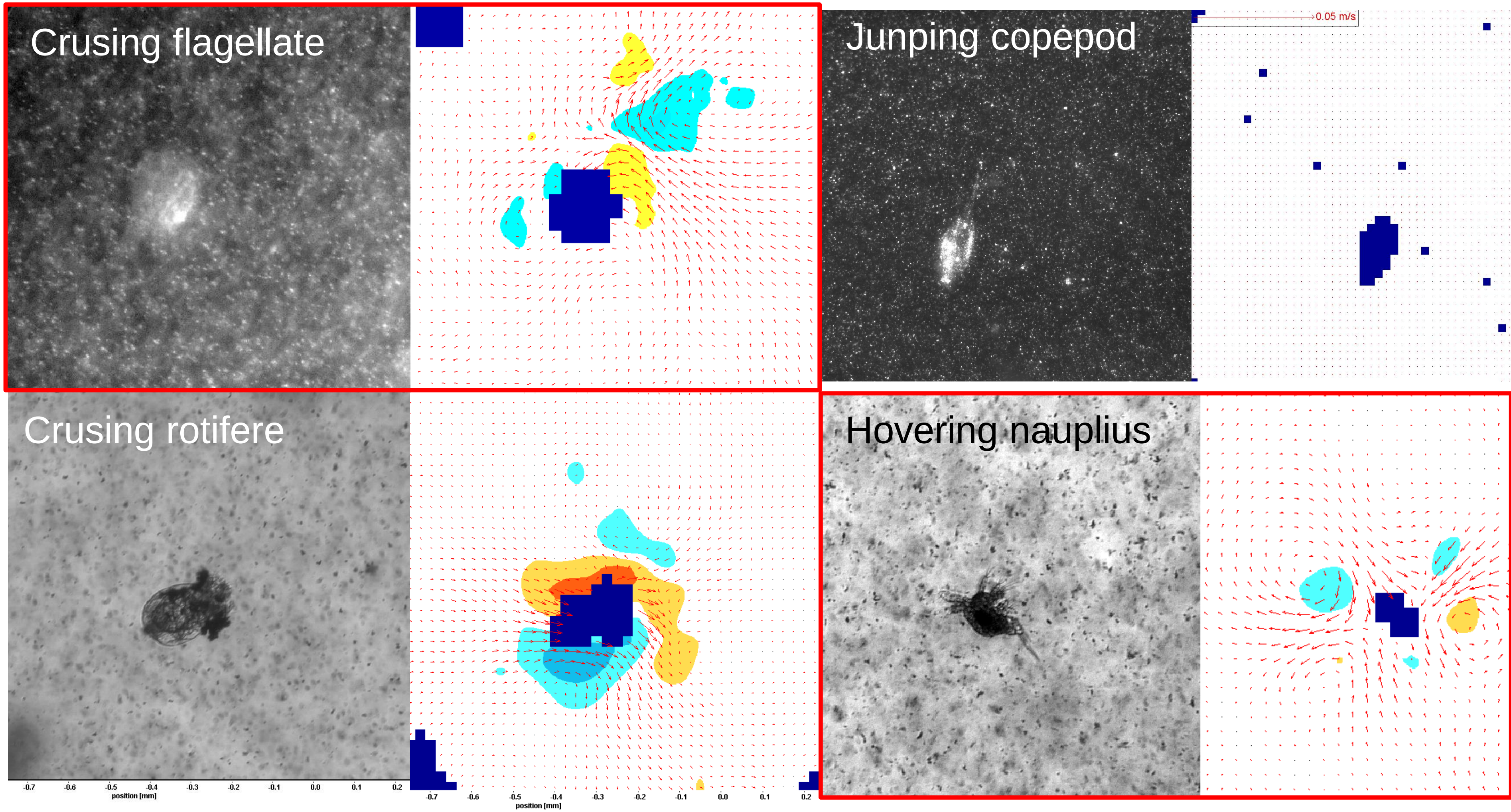






Fluid disturbances

Flow and vorticity fields



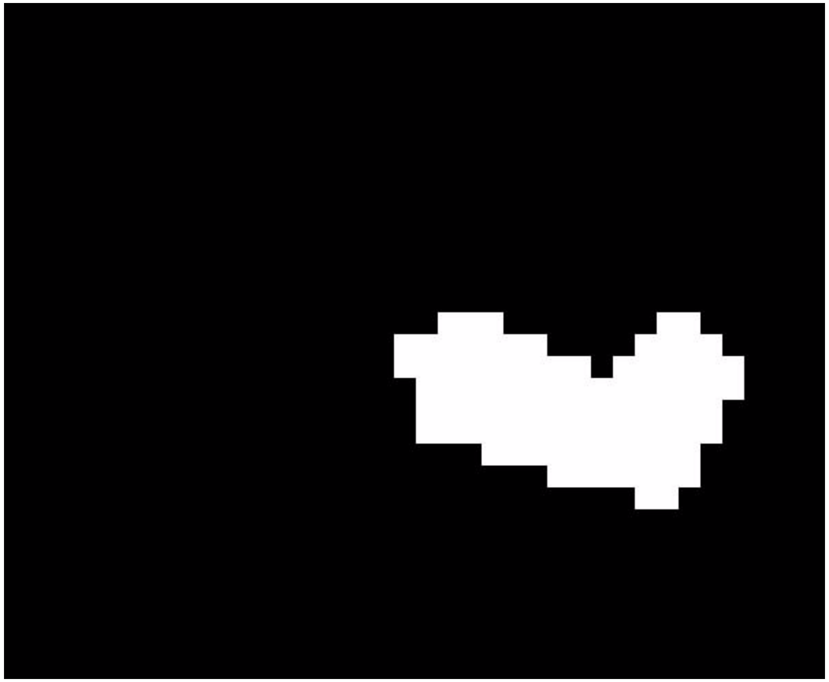
SloMo 1:40

Kiørboe et al. *PNAS* 2014

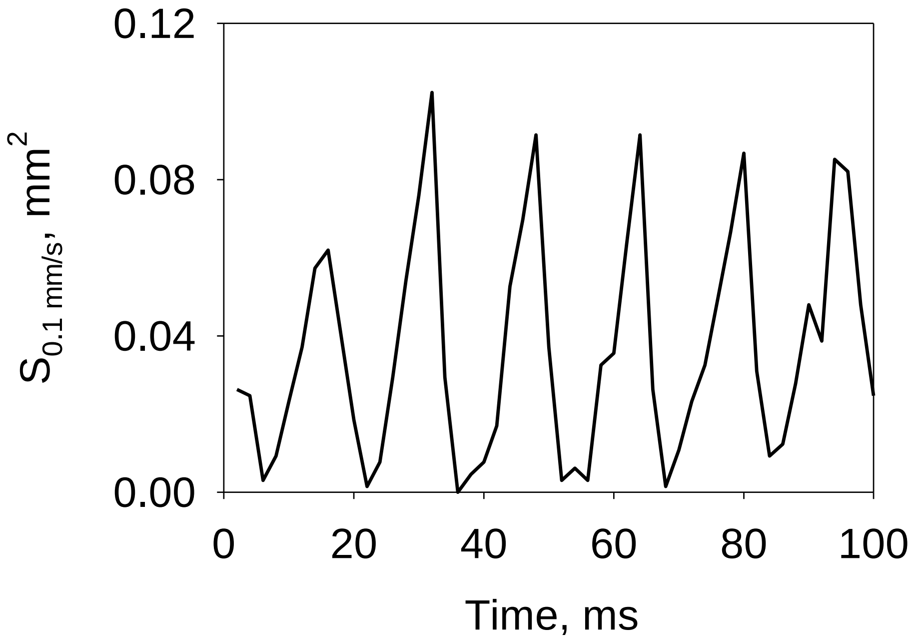
Extension of flow field: temporal variation

Area with imposed velocities > U* (= Predator encounter cross section)

Oxyrrhis marina



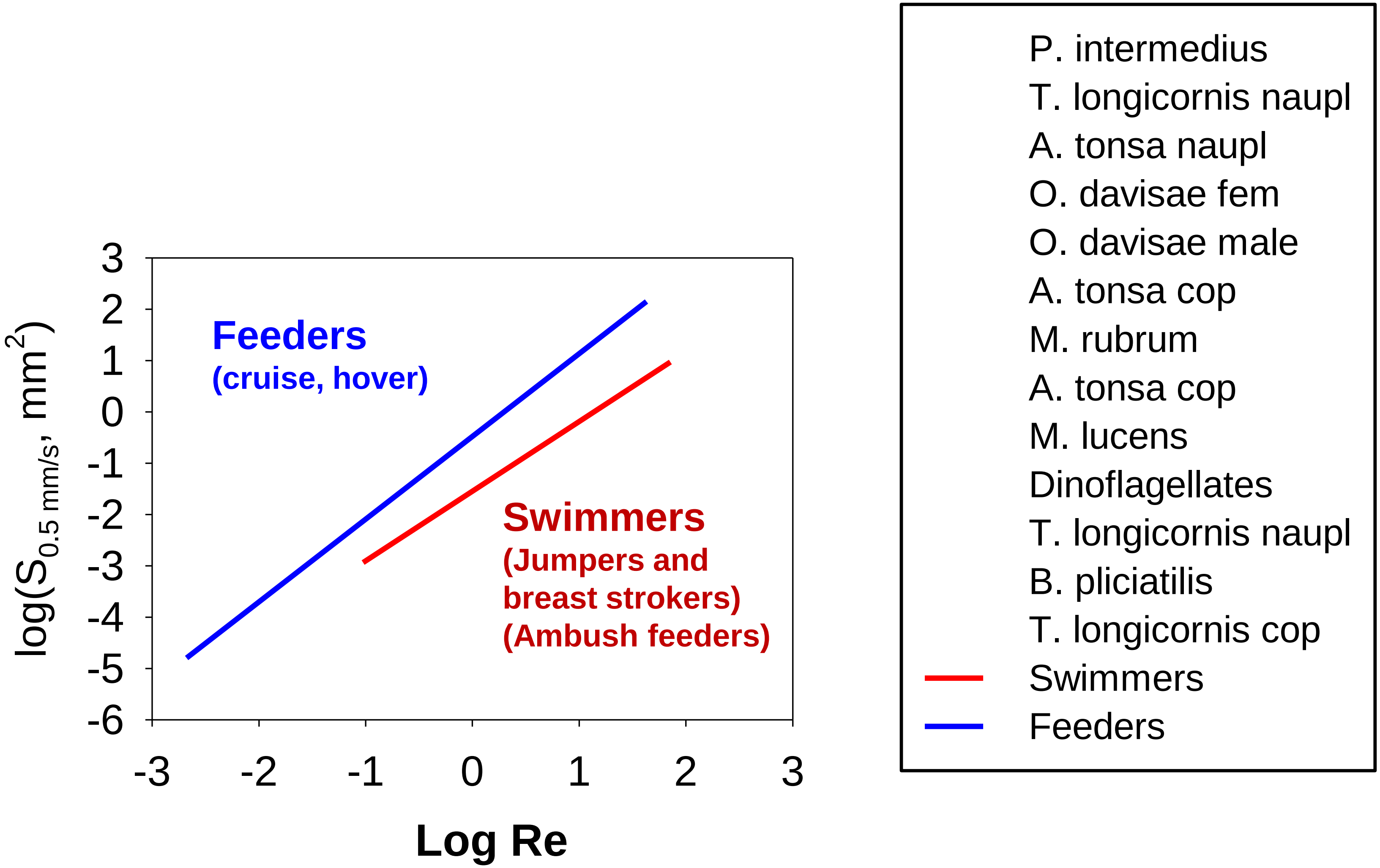
U* = 0.08 mm/s
SloMo1:40



Kiørboe et al. *PNAS* 2014

Peak extension of flow field

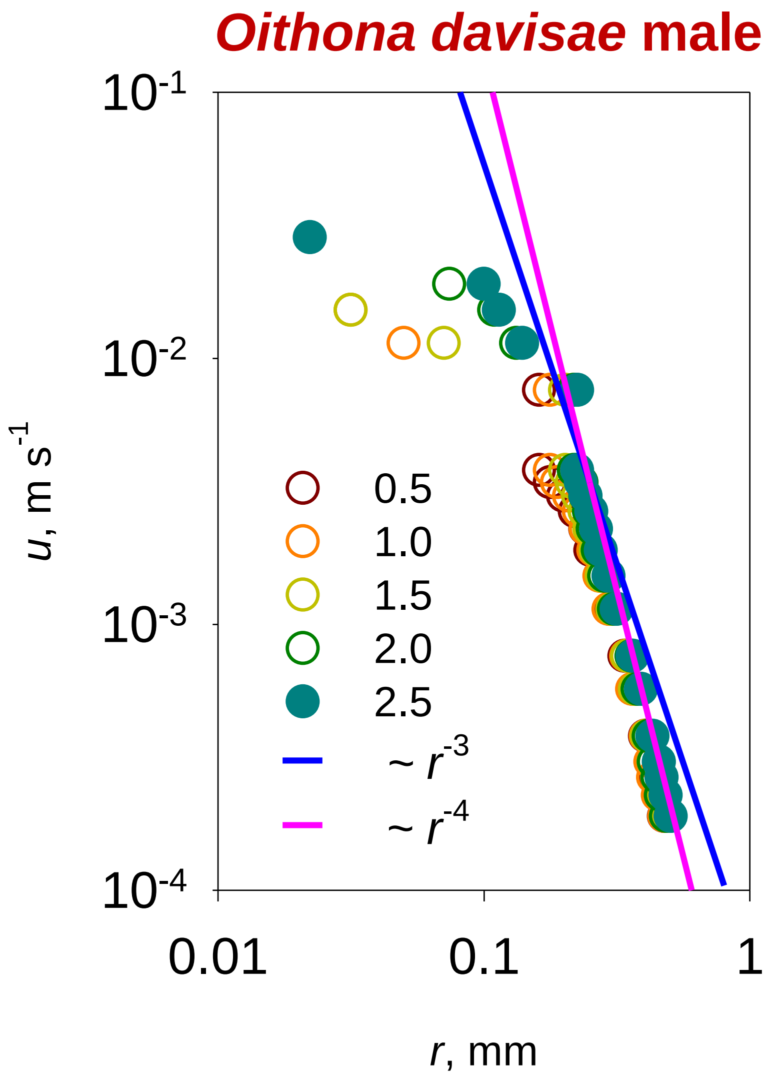
Feeders generate larger flow fields than swimmers

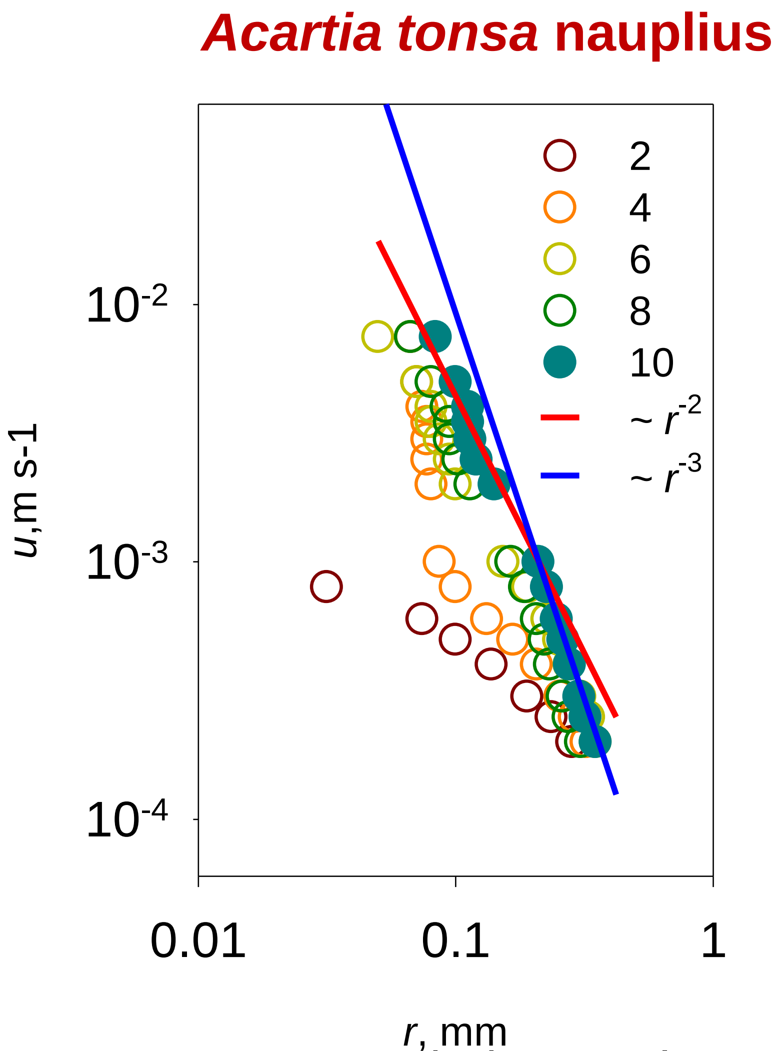


Kiørbœ et al. *PNAS* 2014

Spatial attenuation of flow fields

During peak of power stroke (closed symbols)





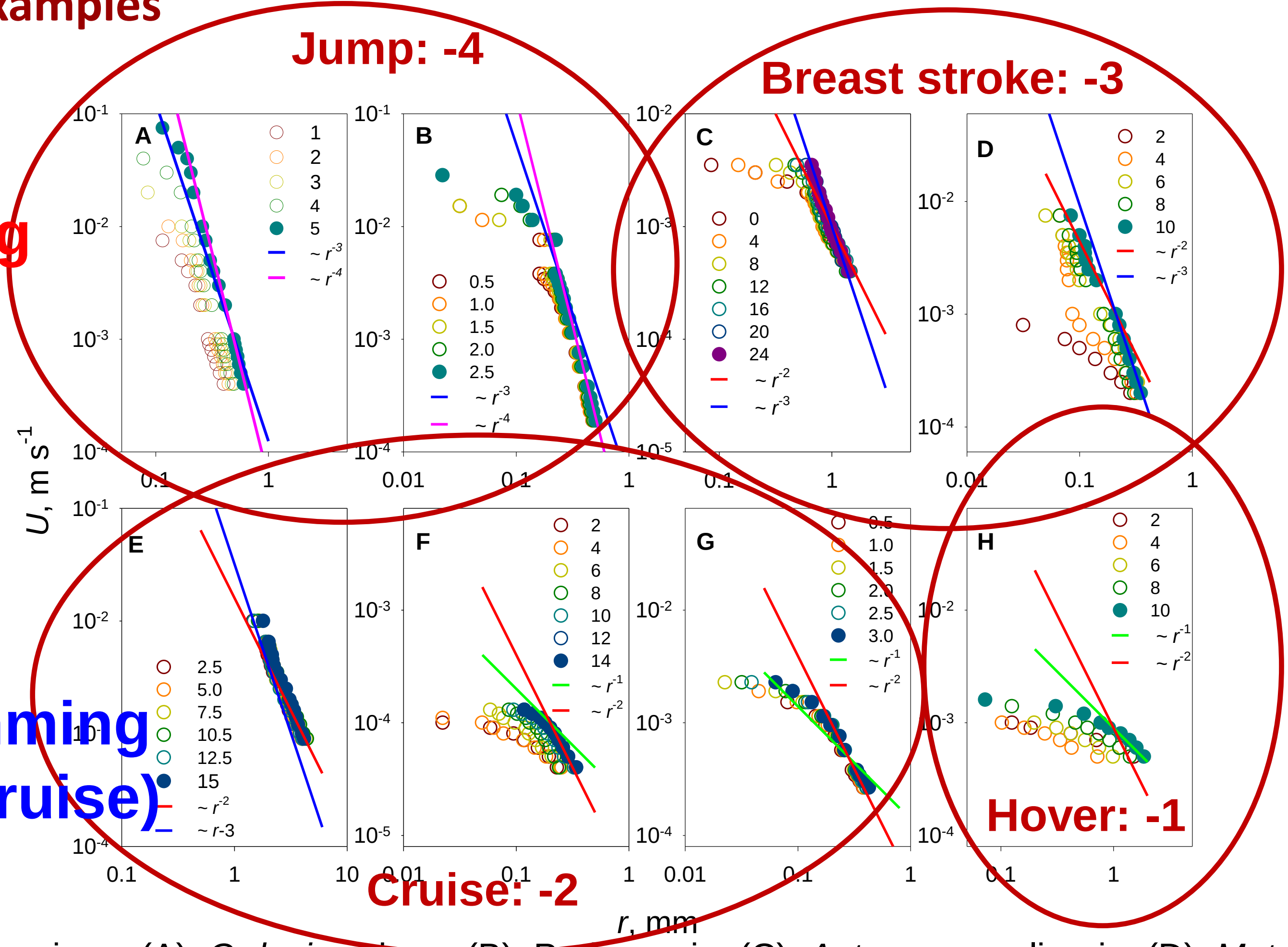
Kiørboe et al. *PNAS* 2014

Spatial attenuation

More examples

Swimming (ambush)

Feeding and swimming (Hover, Cruise)

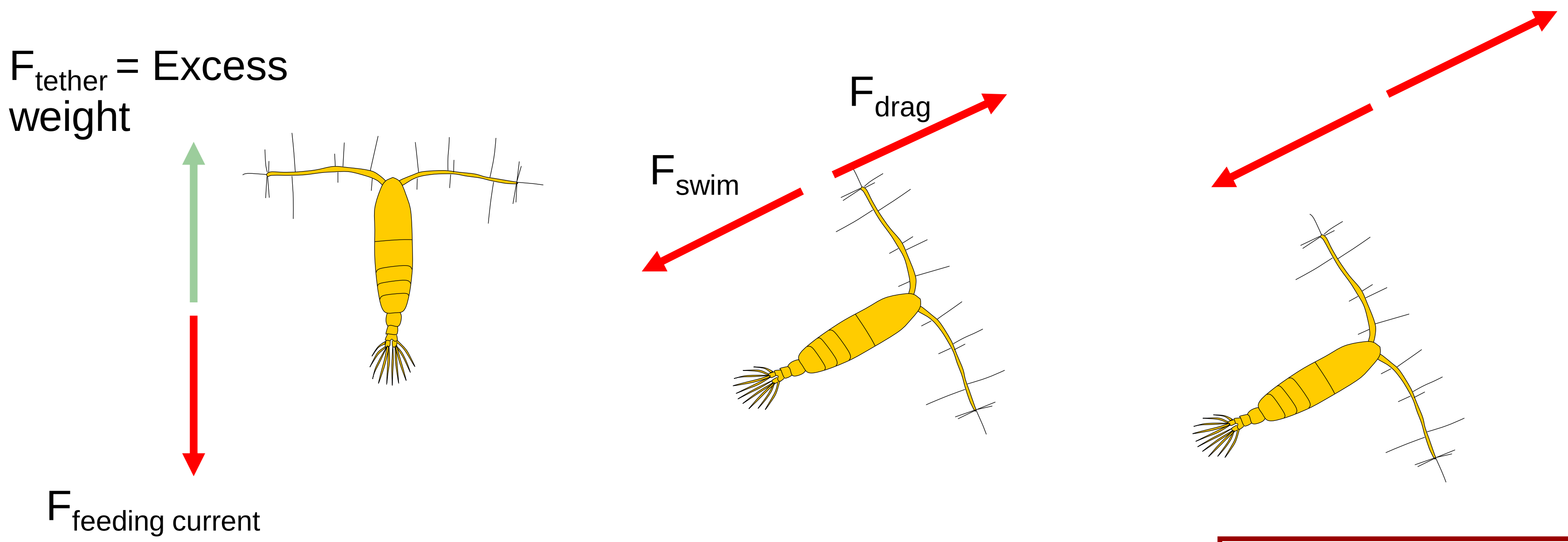


A. tonsa jump (A); *O.davisae* jump (B); Podon swim (C); *A. tonsa* naupli swim (D); *Metridia* cruising (E); Dinoflagellate cruising (F), *Temora* nauplius feeding current; *Temora* copepodit hovering

Kiørboe et al. *PNAS* 2014

Idealized models

R^{-1}	R^{-2}	R^{-4}
Hovering (feeding current) (negatively boyant)	Crusing (Neutrally boyant)	Jumping (Jump)

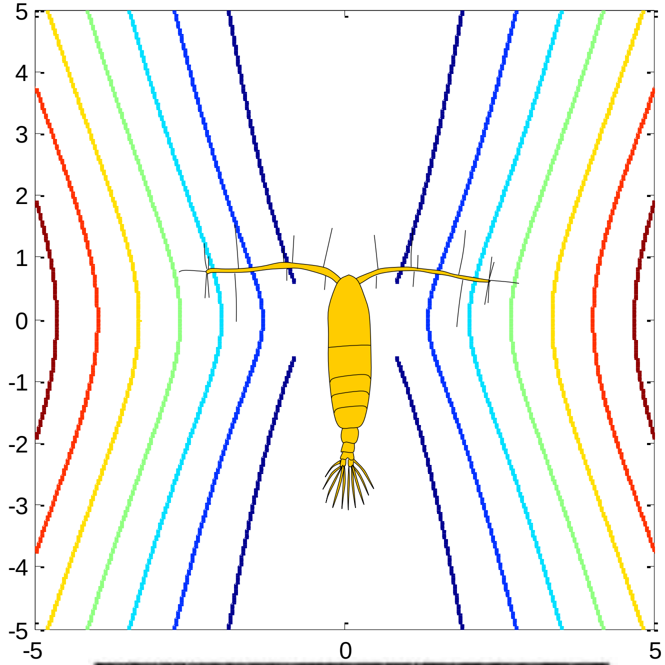


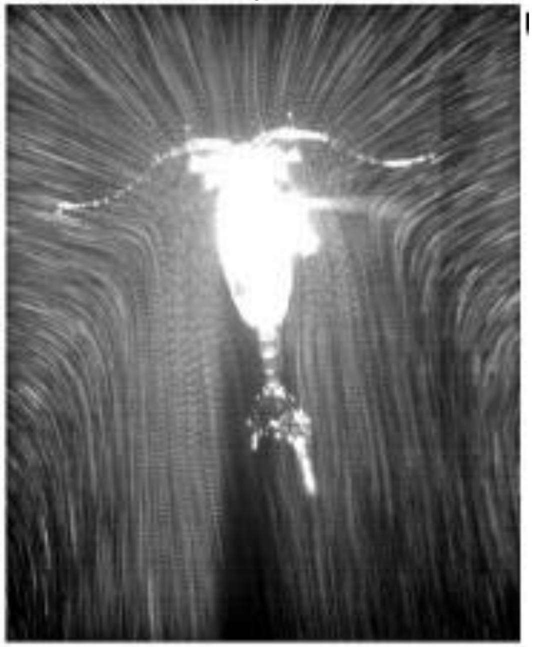
$F_{feeding\ current}$ **STOKESLET**	$F_{drag} = F_{swim}$ **STRESSLET**	$F_{drag} = F_{swim}$ **IMPULSIVE STRESSLET**

Only red forces act on the water

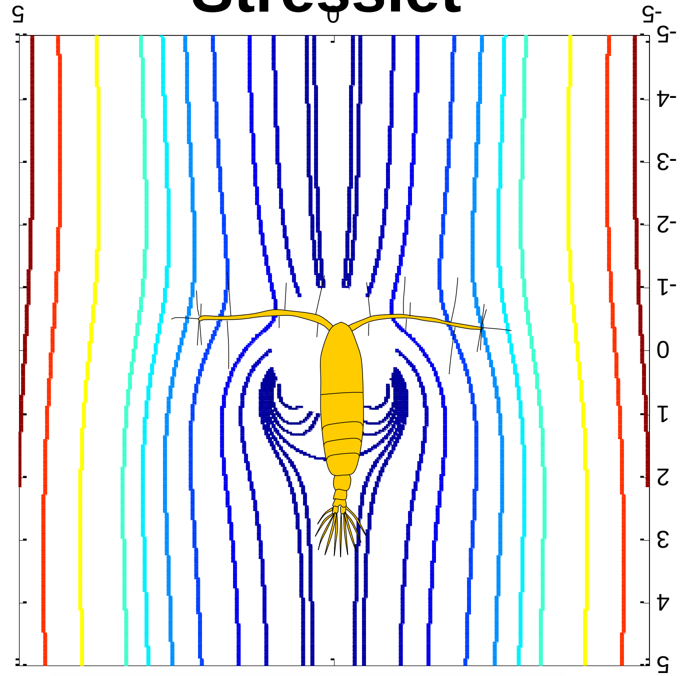
Kiørboe et al. *PRSB* 2010

Stokeslet





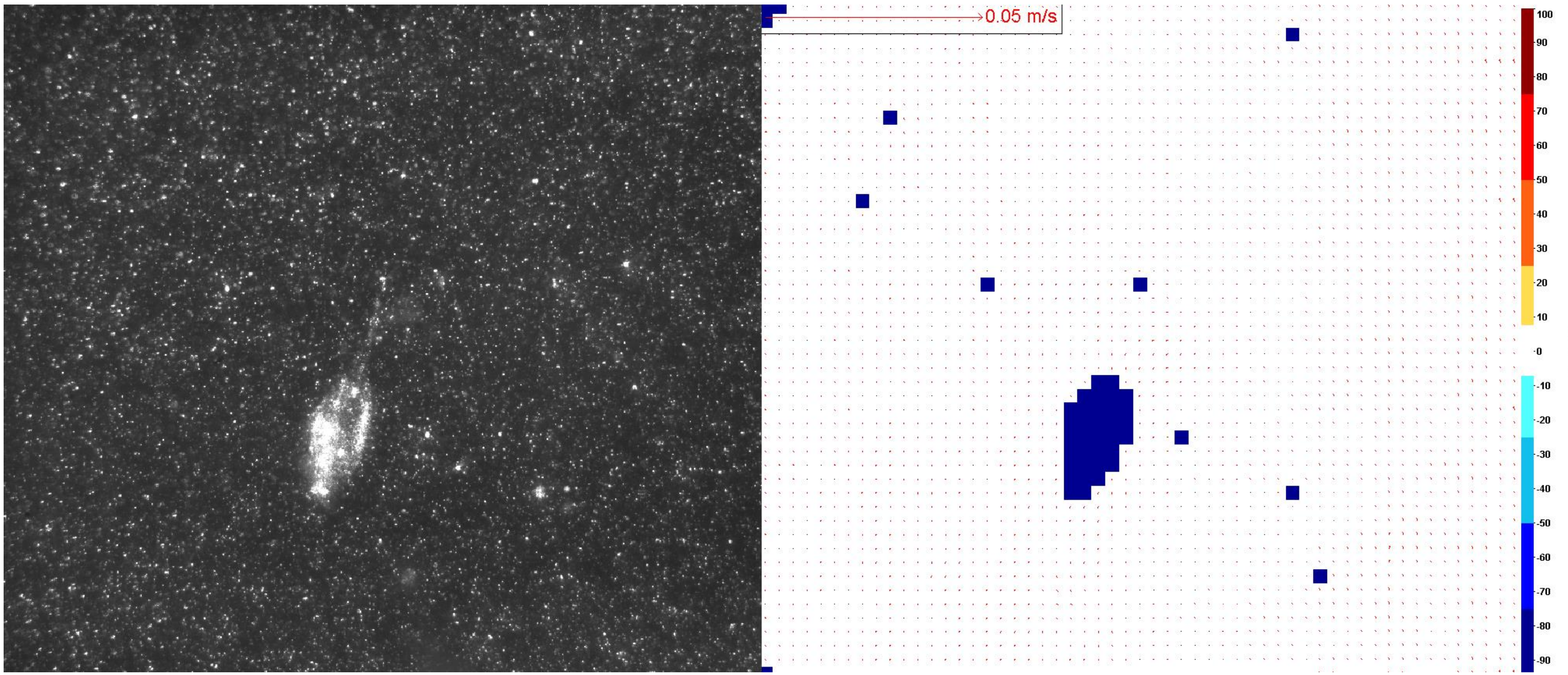
Stresslet



Catton et al.
JEB 2007

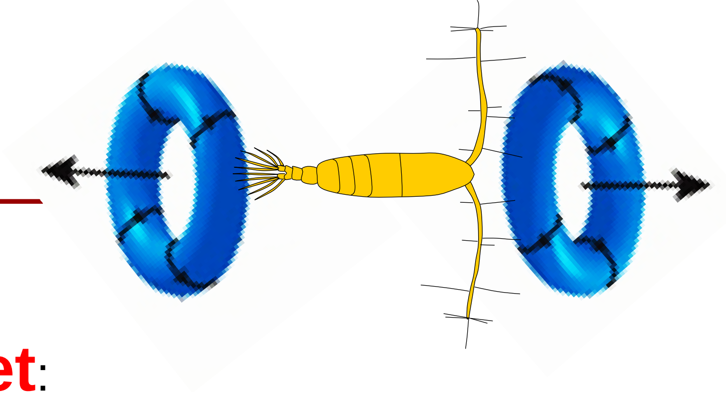
Jumping copepod

Predicted vs observed



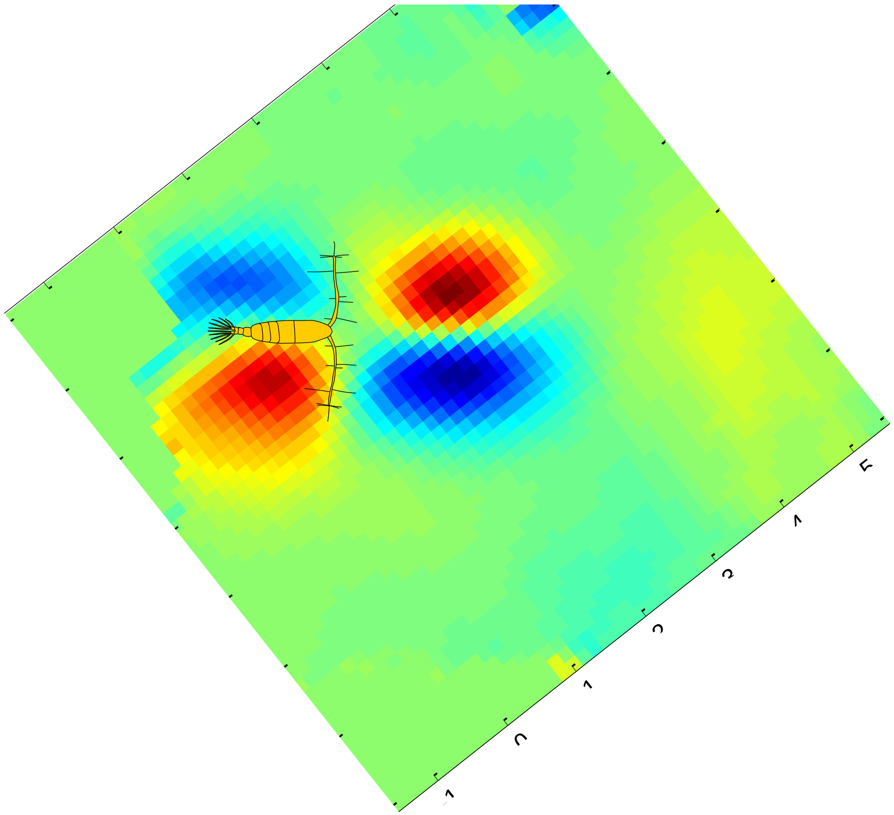
Jumping copepod

Predicted vs observed

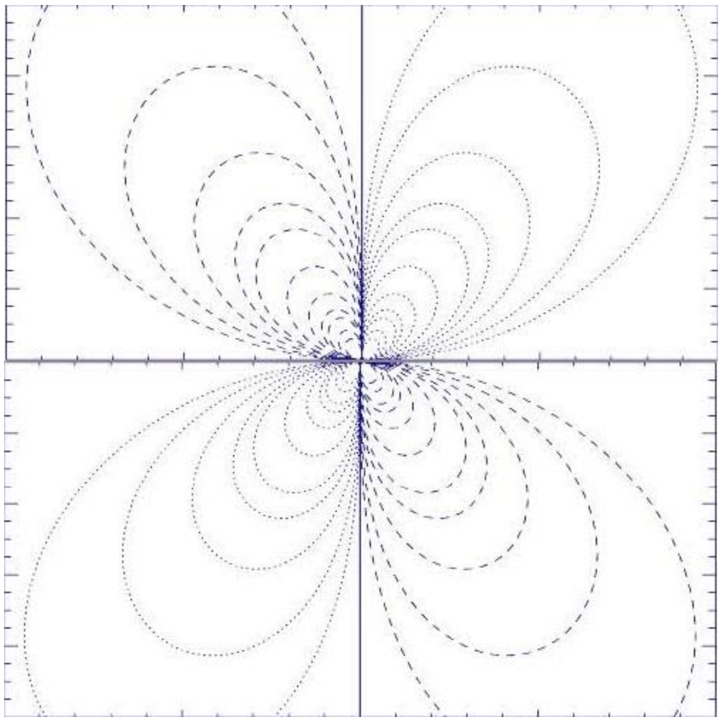


Impulsive stresslet:

Observed vorticity



predicted vorticity

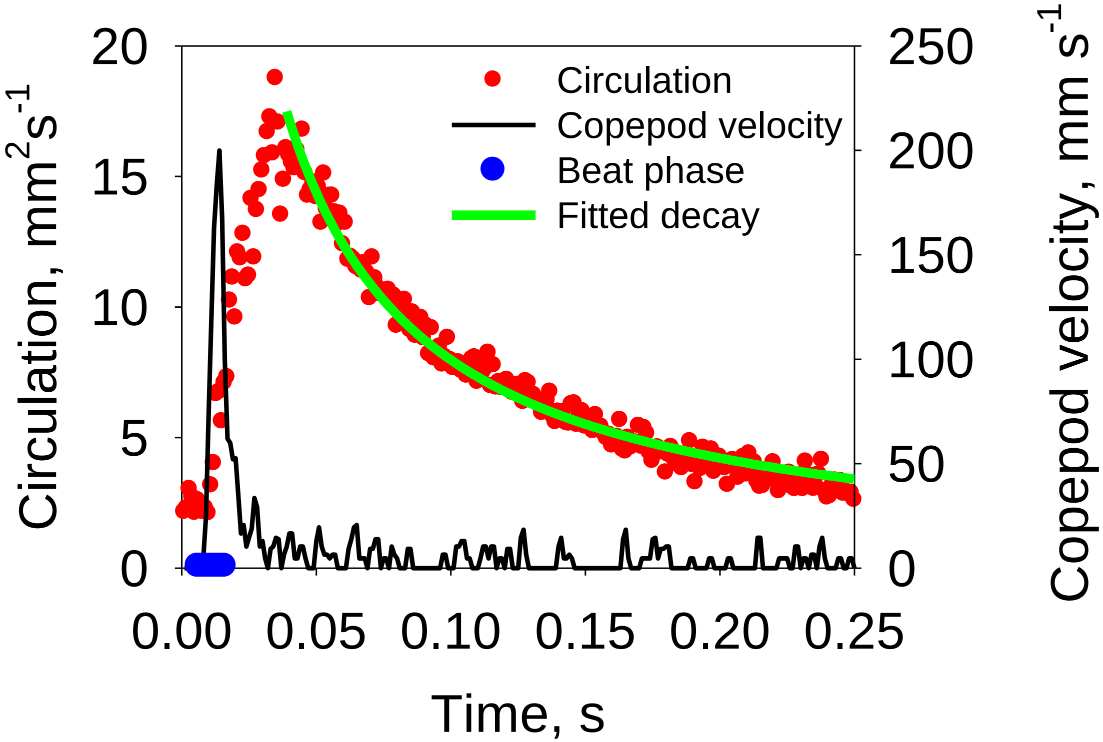


Kiørboe et al. *Proc Roy Soc B* 2010; Jiang & Kiørboe *J Exp Biol* 2011

Model predicts decay of vortex

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

Circulation: spatial integral of vorticity

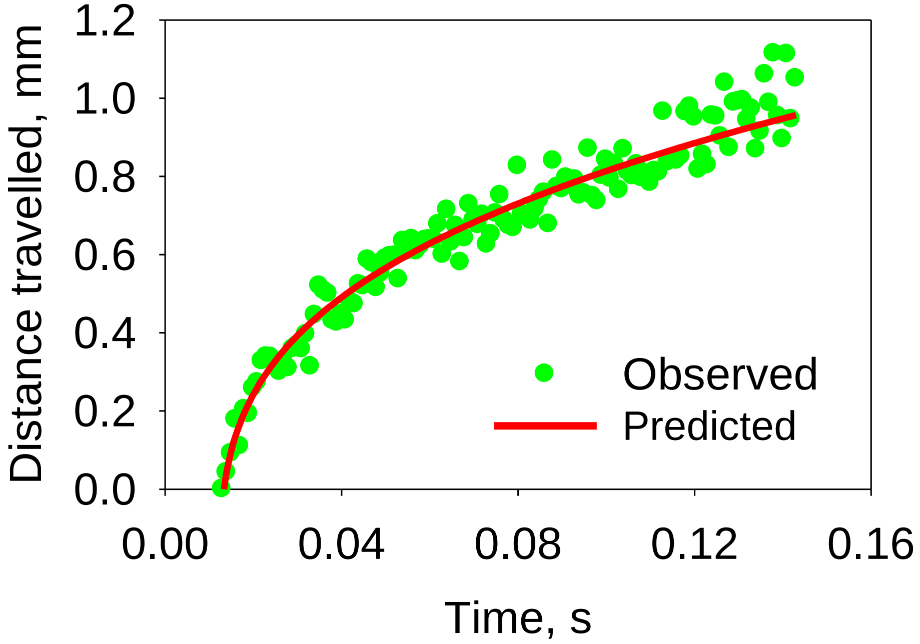


Estimated momentum of wake: 10^{-8} kg m s^{-1}

Kiørboe et al. *Proc. Roy Soc B* 2010

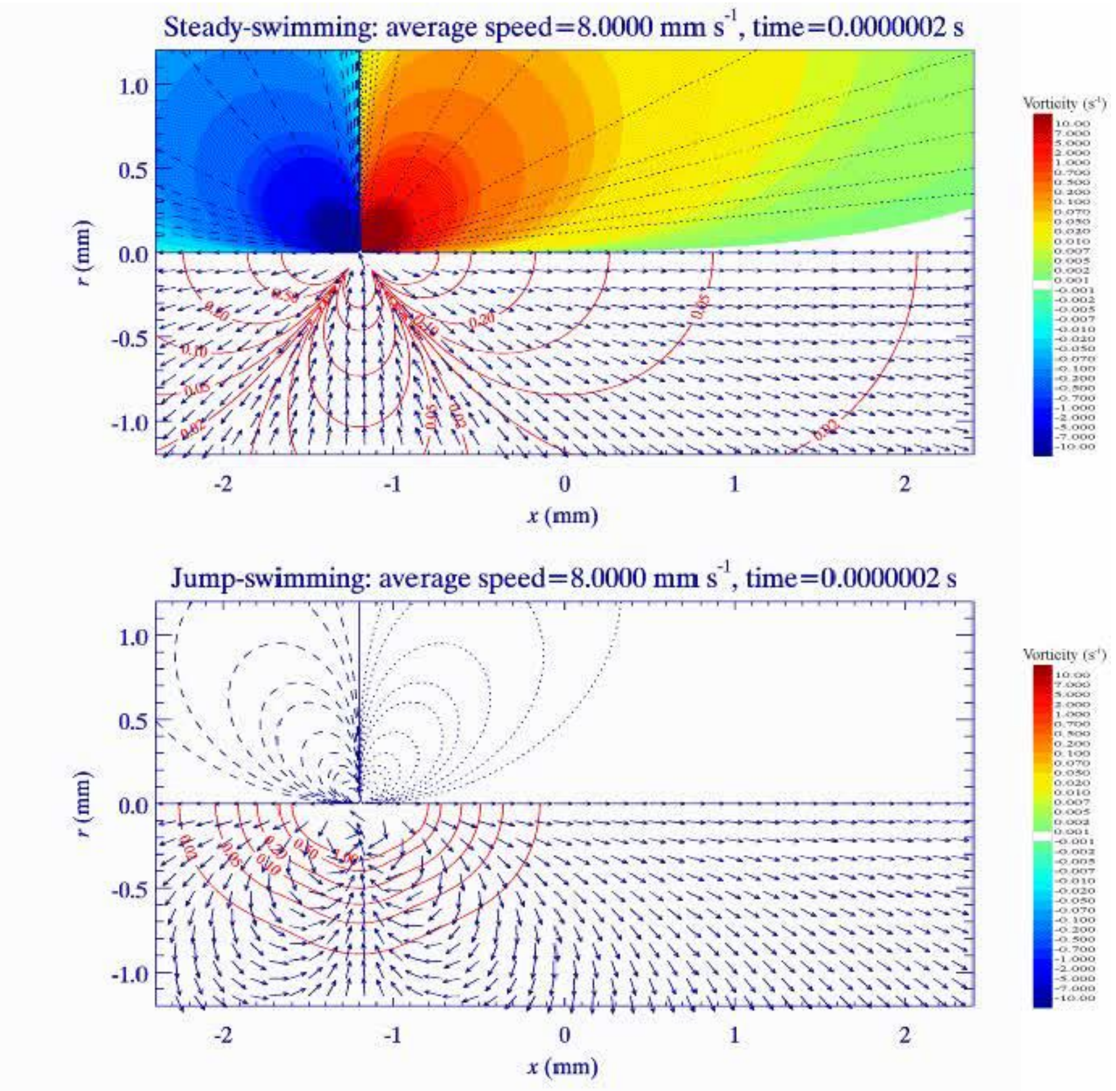
Model predicts translation of vortex

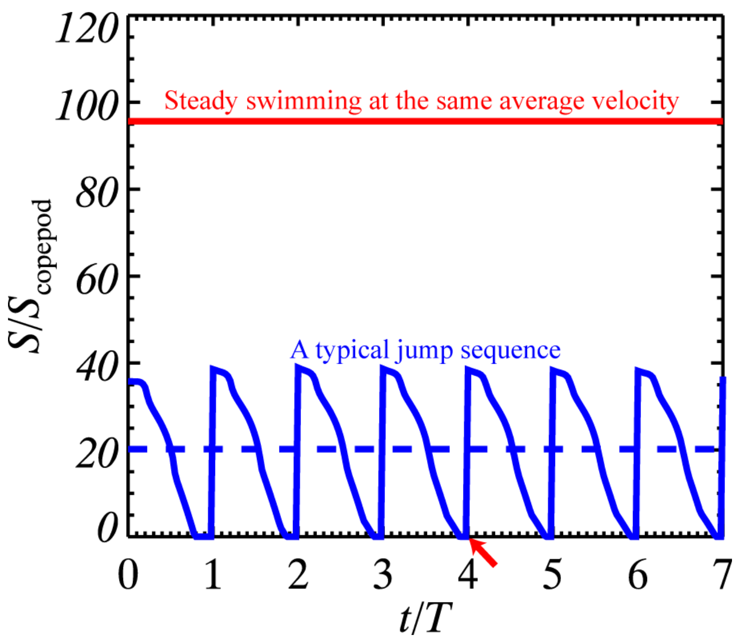
$$L(t) = \left(2\nu(t - t_0) + \left(\frac{2I}{\pi}\right)^{1/2} (t - t_0)^{1/2}\right)^{1/2}$$



Kiørboe et al. *Proc. Roy Soc B* 2010

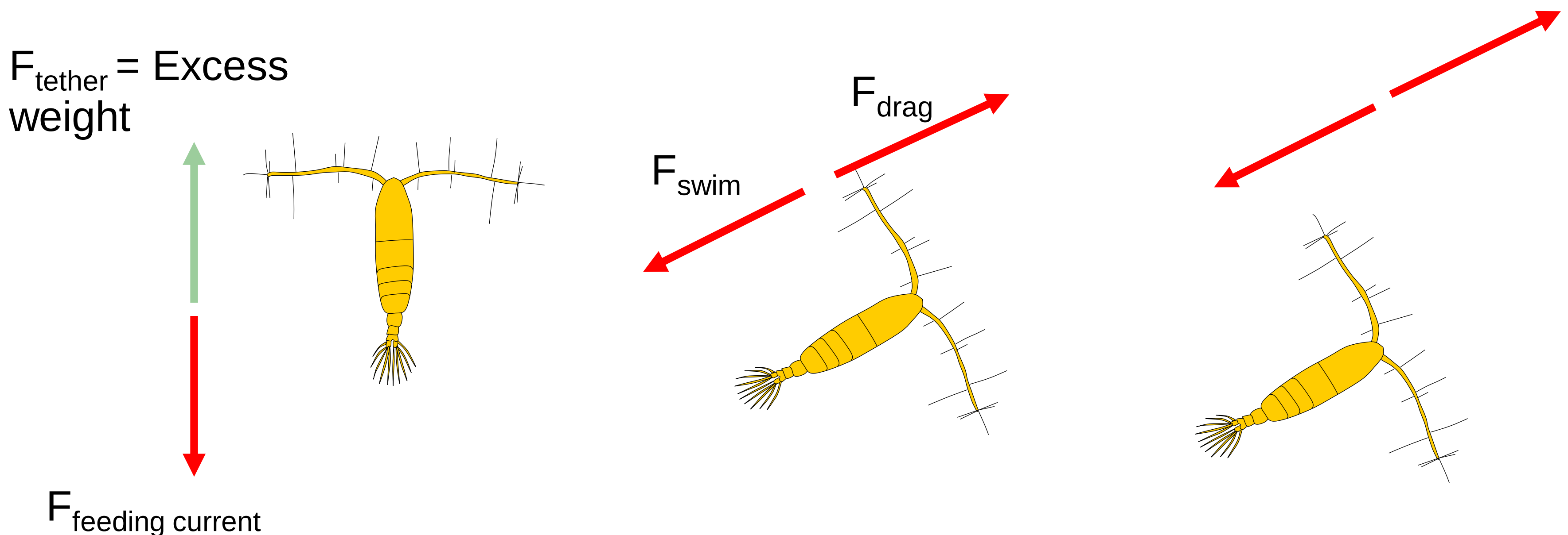
Two swimming modes





Idealized models

R^{-1}	R^{-2}	R^{-4}
Hovering (feeding current) (negatively boyant)	Crusing (Neutrally boyant)	Jumping (Jump)



$F_{feeding\ current}$ **STOKESLET**	$F_{drag} = F_{swim}$ **STRESSLET**	$F_{drag} = F_{swim}$ **IMPULSIVE STRESSLET**

Only red forces act on the water

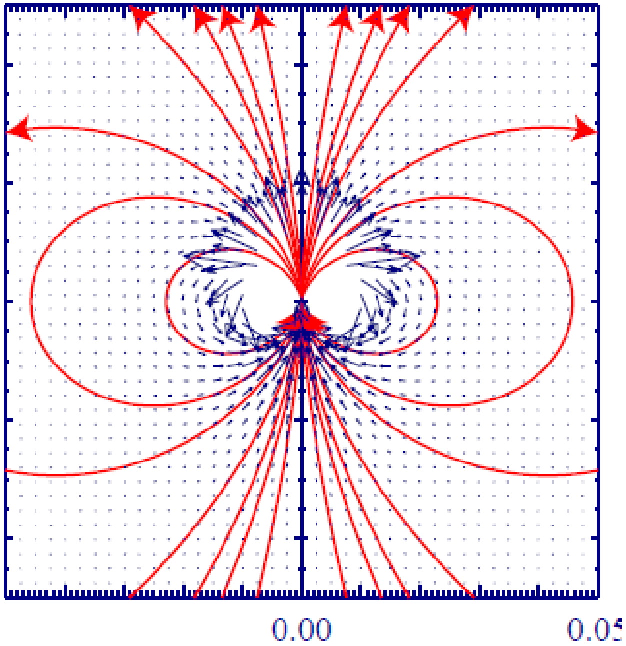
Kiørboe et al. *PRSB* 2010

Breast stroke: Quadropole

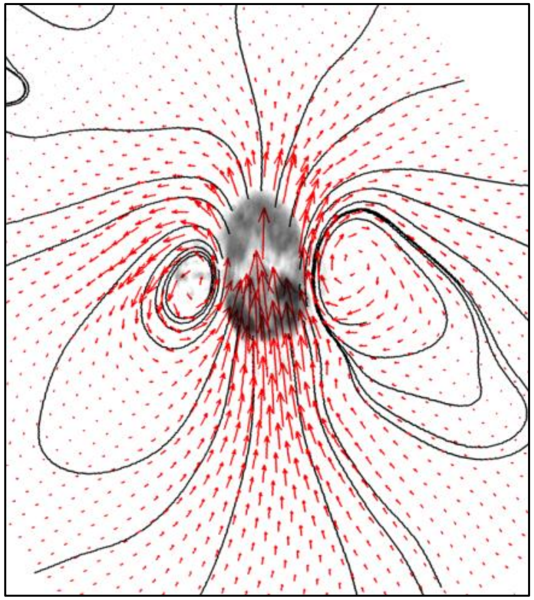
R^{-3}

Breast stroke swimming: appendages follow streamlines of a potential dipole (quadropole)

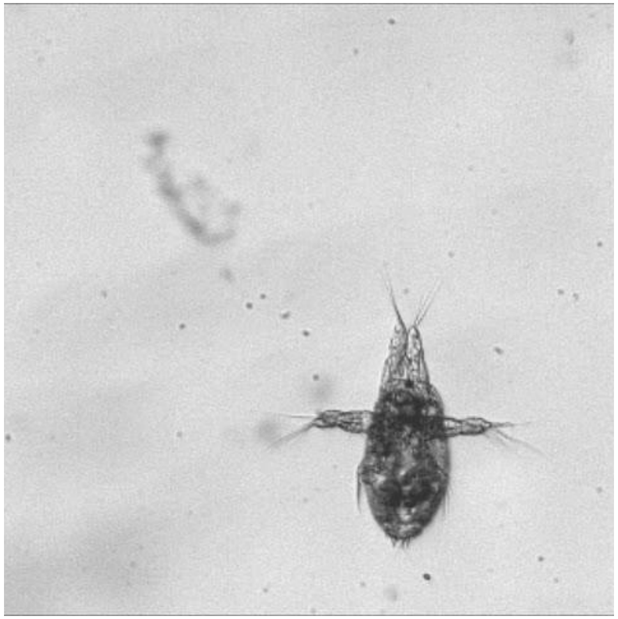
Predicted streamlines



observed streamlines



Breast swimming nauplius

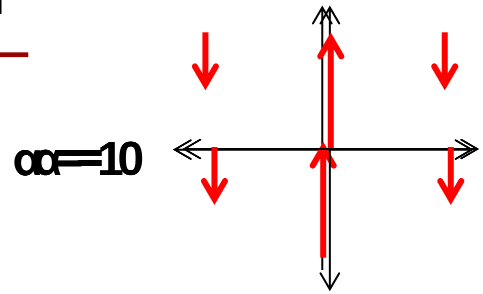


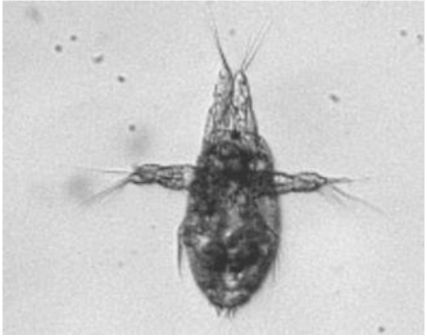
Kiørboe et al. *PNAS* 2014; Andersen et al. *PRE* 2015

Three Stokeslet model

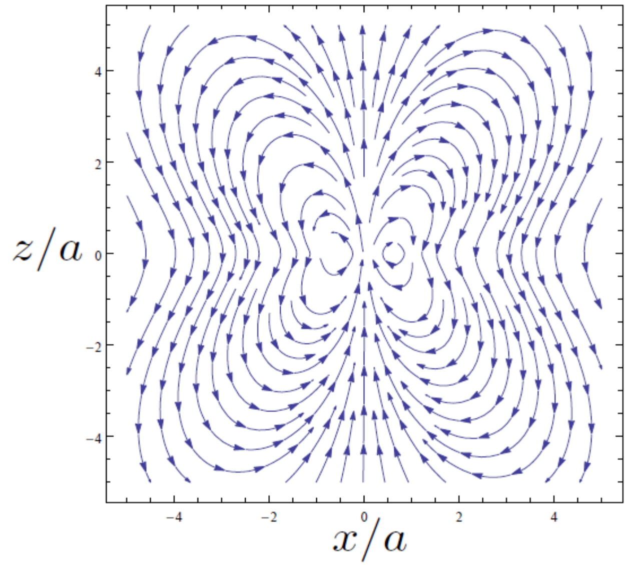
Align the forces

Force distribution





Flow field

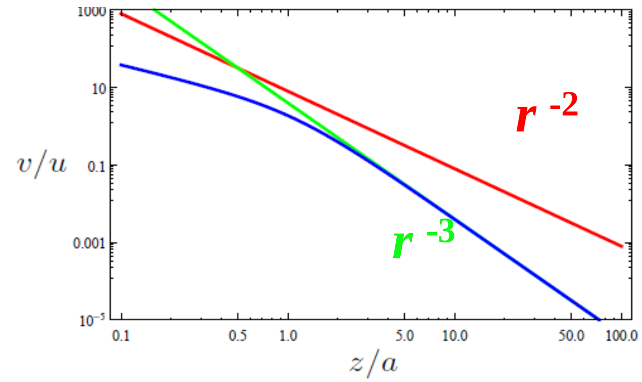


Spatial attenuation

Modelled

Stresslet

Quadropole



Andersen et al in prep

Bulk properties of flow

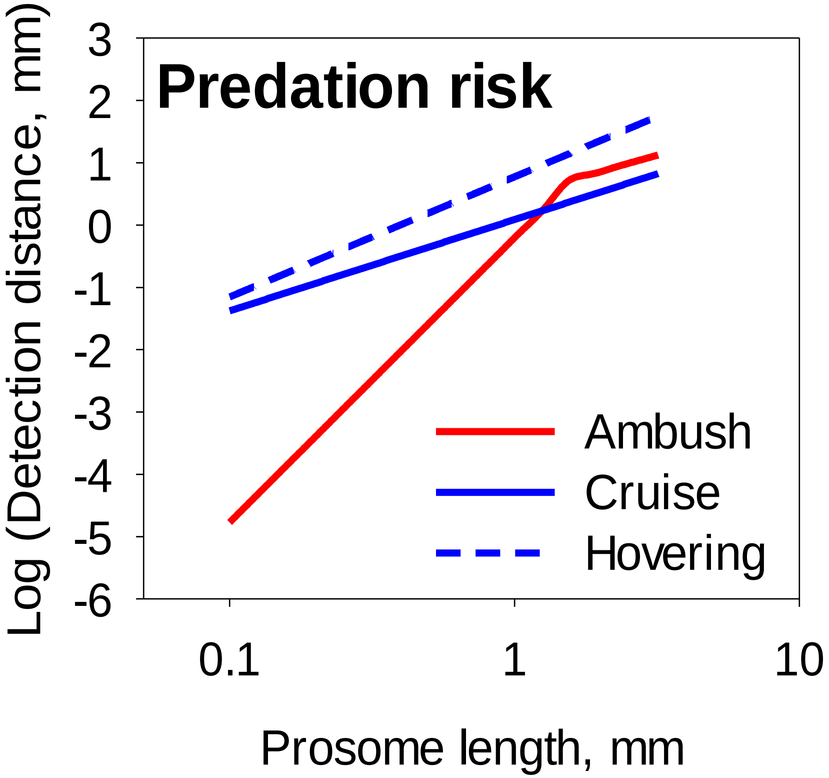
Spatial flow attenuation from idealized , taxa-transcending models

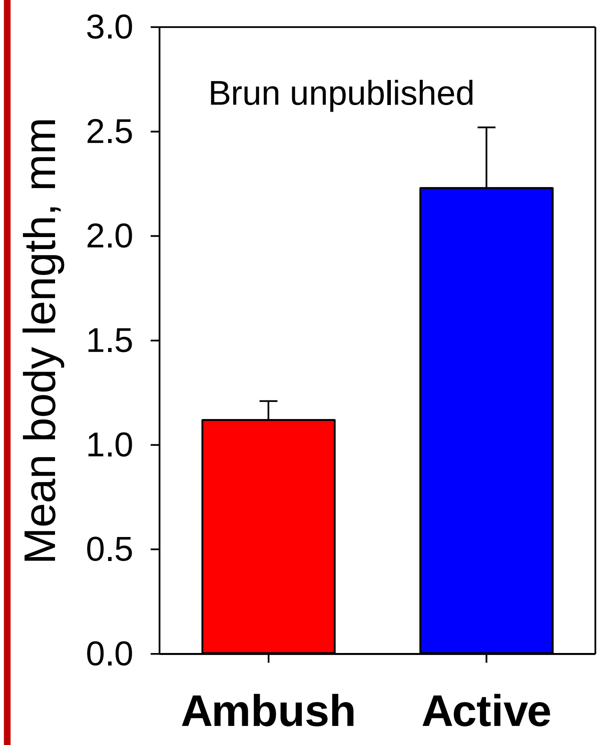
Behaviour	Purpose	Model	Attenuation
Hovering	Feeding	Stokeslet	R^{-1}
Cruising	Feeding & locomotion	Stresslet	R^{-2}
Ambush (Jumping)	Locomotion	Impulsive stresslet	R^{-4}
Ambush (Breast stroking)	Locomotion	Quadropole (potential dipole)	R^{-3}

we can rationalize and – therefore – generalize the observed fluid disturbances

Feeding tradeoffs

Predation risk estimated from simple <u>generic</u> fluid mechanical models



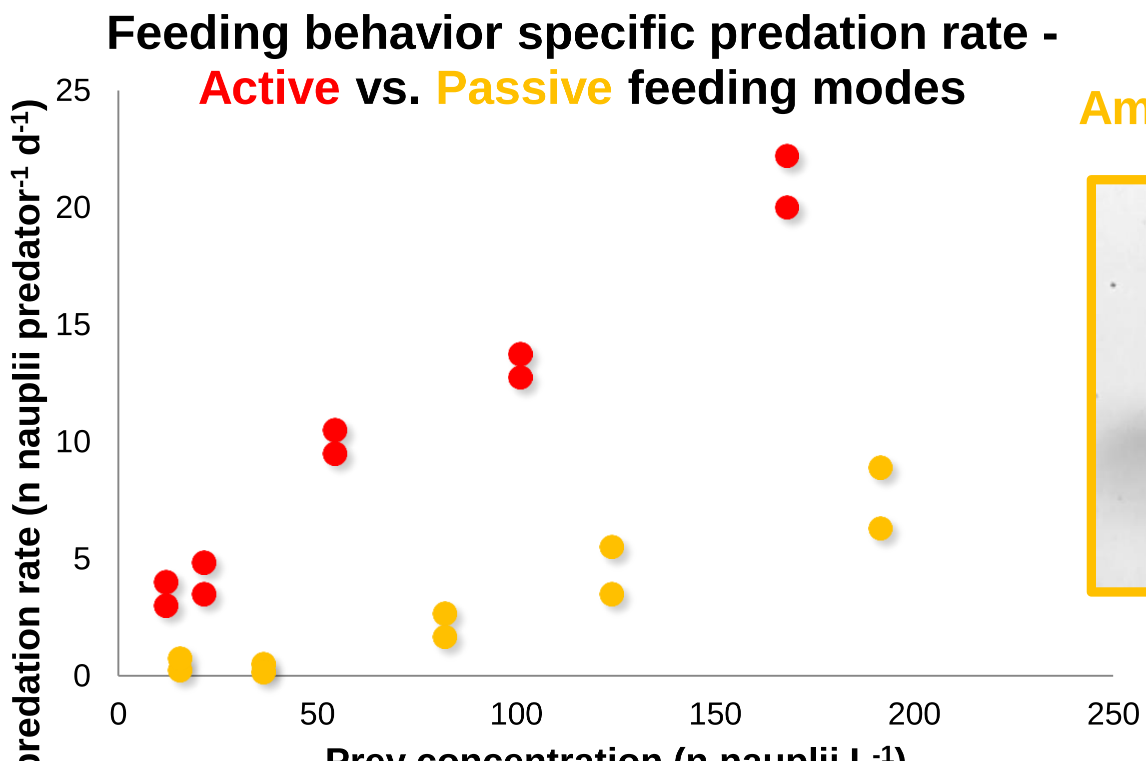


Kiørboe et al. *Proc Roy Soc B* 2010

Feeding tradeoff: Experimental testing

Rheotactic predator feeding on active and passively feeding nauplii

Active feeder



Ambush feeder

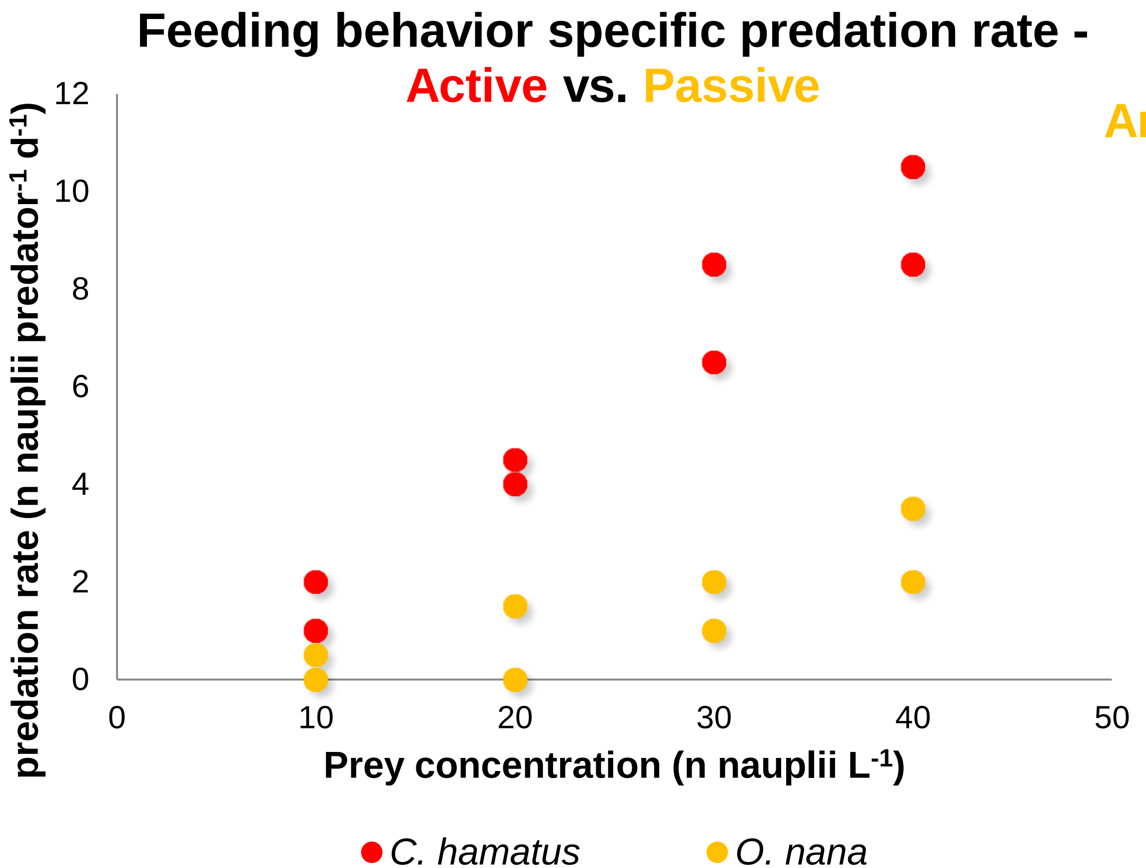
THE MORTALITY RISK OF THE ACTIVE FEEDER IS MUSCH HIGHER THAN THAT OF THE PASIVE FEEDER

Someren Gréve and Almeda unpublished

Feeding, swimming, and predation risk

Experimental testing: Large copepod feeding on nauplii

Active feeder



Ambush feeder

SAME RESULT FOR DIFFERENT SET OF PREY

Someren Gréve et al unpublished

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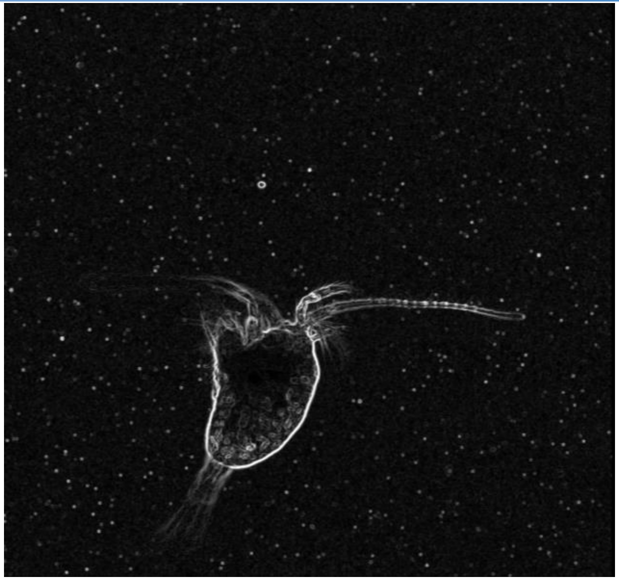

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