

# Tiny Giants - Mathematics Looks at Zooplankton

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March 31st, 2022, Dresden, Germany



## Chief Collaborator (2009-present)



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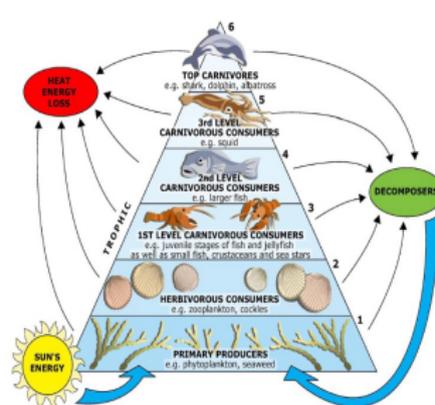
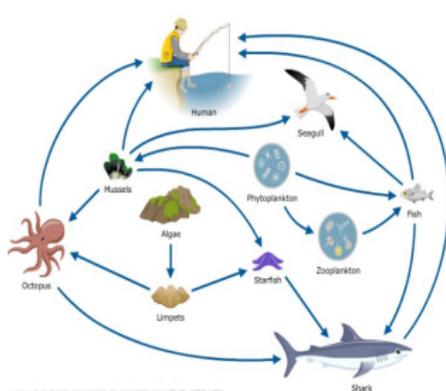
- ▶ What is plankton, why do we care?
- ▶ Olfaction in a viscous environment
- ▶ Near-field feeding currents and particle sensing
- ▶ Outlook

# Plankton (Victor Hensen, 1887)



πλαγκτός - “wanderer, drifter” - follow water currents on the kilometer scale, but some are able to swim hundreds of meters on their own daily. They inhabit every freshwater and marine habitat on earth. Two subgroups:

- ▶ phytoplankton - carry out  $\approx 70\%$  of all photosynthesis
- ▶ zooplankton - heterotrophic, crucial link in the marine food web



# Zooplankton diversity



- ▶ Zooplankters have sizes between 1  $\mu\text{m}$  and 200 mm.
- ▶ They come from a large number of phyla: cnidarians (e.g. jellyfish), rotifera, arthropoda (e.g. **crustaceans**), chordata (e.g. fish larvae).

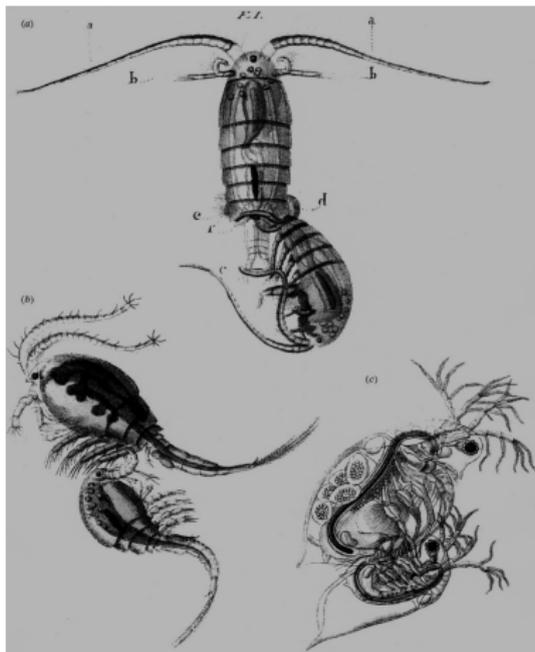
# Plankton ecology and emerging dangers

- ▶ anthropogenic global climate change
- ▶ shifts of biogeographic boundaries, leading to changes in species distributions
- ▶ ocean acidification
- ▶ invasive species

# Mathematical modeling approaches

- ▶ population dynamics to study nutrient cycles, food web dynamics, parasite infestations
- ▶ size and age-structured models (i.e. PDEs)
- ▶ individual-based models, simulations
- ▶ computational fluid dynamics of individual swimmers, colonies and swarms
- ▶ fractal analysis of recorded swimming paths

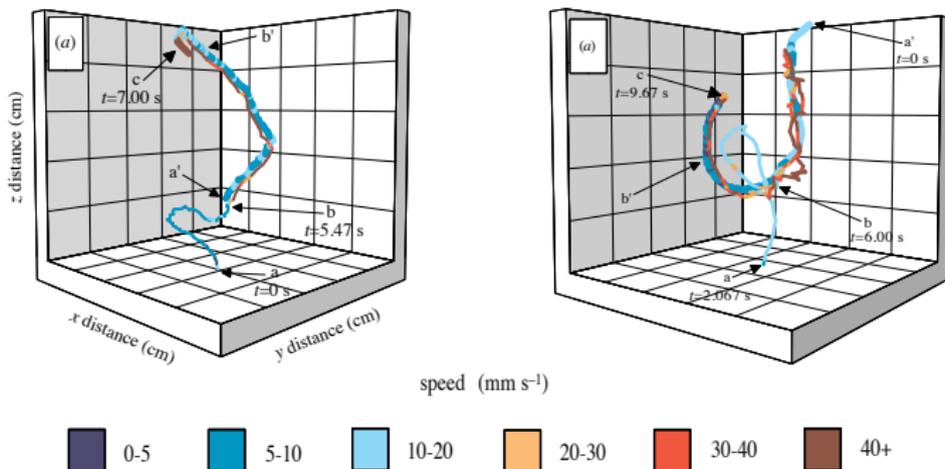
# Sex in the deep sea



Louis Jurine, *Histoire de Monocles*, Geneva (1820)

It is dark, the dimensions are three, the mate is hundreds of body lengths away . . . **How to find each other?**

# Mate tracking in *Temora longicornis*

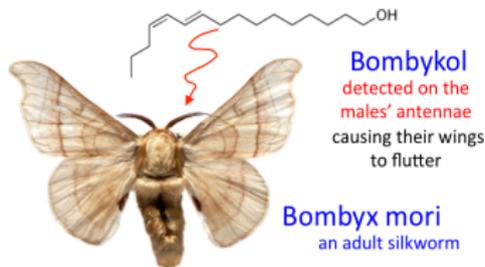


Trails of females and males - “Fat” trail = female, “thin” trail = male. In 22 out of 27 observations when the initial swimming direction was incorrect the male turned around (81 %).

Doall et al. *Phil. Trans. R. Soc. Lond. B* **353**:681-689 (1998)

# Pheromones

φέρω - “to bear”, όρμή - “impetus”



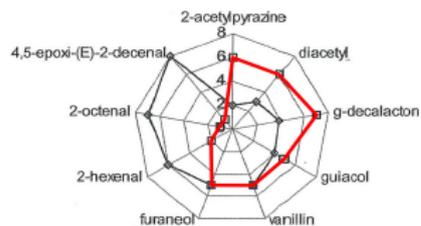
Butenandt *et al.* H-S. Z. Physiol. Chem. **324** (1959)

Sex pheromones in copepods have been proposed by Katona in 1973, but so far none haven been identified chemically.

# Evidence of backtracking

If the male initially picks the wrong direction for pursuit, it is able to correct that and to follow the trail in the correct direction. Thus the trail is not a mere curve but a vector field.

**Does the “age” of the smell have to do with it?**



K. Gassenmeier (Givaudan S.A., Switzerland)

Fresh cookies smell differently (better!) than stale ones.

# Building the trail

The female is moving with constant velocity  $U$ , and produces compound(s)  $i = 1$  or  $i = 1, 2$  respectively. We assume they have

- ▶ same production rates  $Q$ ,
- ▶ same diffusion rates  $D$ ,
- ▶ different decay rates  $k_i$  (if more than one).

The advection-diffusion equation for the concentration  $u(x, y, z, t)$  is given by

$$\frac{\partial u}{\partial t} + U \frac{\partial u}{\partial x} = D \Delta u - k u,$$

in the moving frame of the female where the constant velocity  $U$  points in the direction of the positive  $x$ -axis.

# One-dimensional reduction

The concentration decays much faster in the directions orthogonal to the  $x$ -axis than along the  $x$ -axis. We obtain the approximation

$$u_i(x) = \frac{Q}{4\pi D_X} \exp(-4k_i x).$$

The male can only detect the “signal” at its present location,  $v_0$ , and remember the signal at one immediately past location,  $v_{-1}$ . If

$$v_0 - v_{-1} < -\delta$$

then the walker changes its direction where  $\delta > 0$  is the minimum detectable change.

The signal is recorded on average every  $\mu$  steps, which is a Poisson-distributed random variable.

# Number of pheromone components

Either we have only a single compound,

$$u(x) = \frac{1}{10x} \exp\left(-\frac{x}{20}\right),$$

or we have two,

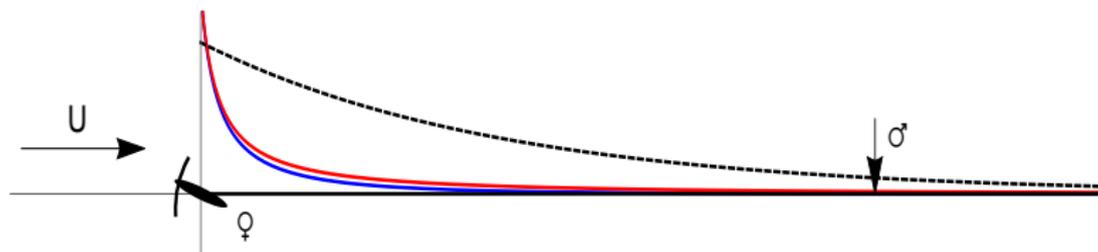
$$u_1(x) = \frac{1}{10x} \exp\left(-\frac{x}{20}\right), \quad u_2(x) = \frac{1}{10x} \exp\left(-\frac{x}{10}\right).$$

and the male can detect the ratio

$$v(x) = \frac{u_2(x)}{u_1(x)} = \exp\left(-\frac{x}{20}\right).$$

For the simulation, the initial direction of the male is always set to “wrong”.

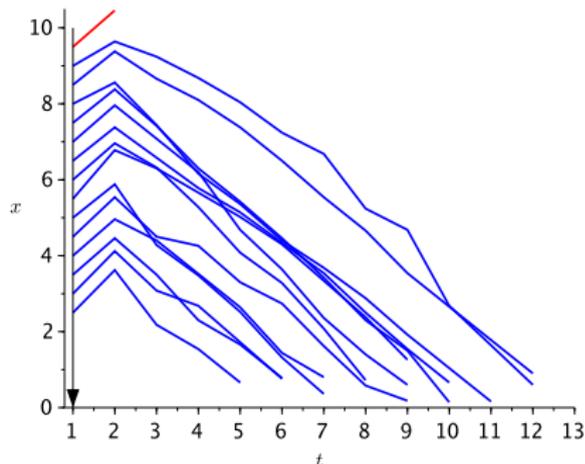
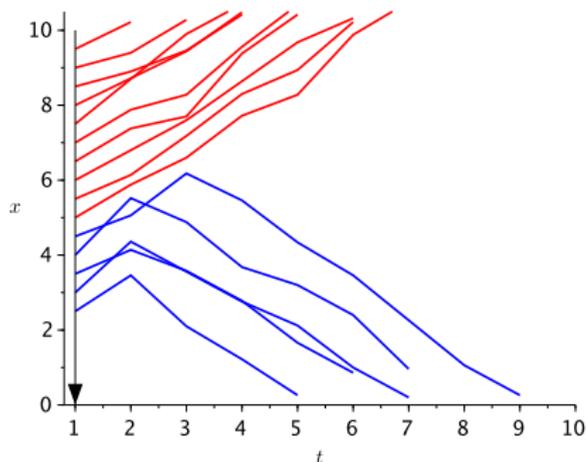
# Concentration and ratio gradients



Red and blue: concentrations of compounds which are  $\ll 1$ ; black: their ratio which is  $O(1)$ .

P. Hinow, J. Yen, J. R. Strickler. Olfaction in a viscous environment: The “color” of sexual smells in *Temora longicornis*. *Sci. Nat.* **104**:46 (2017)

# Increased success rate for ratio detection

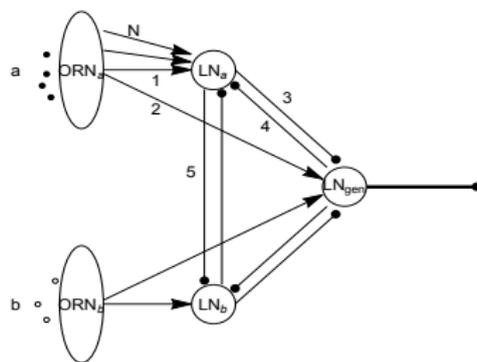


Successful (blue) and unsuccessful (red) searches with single compound,  $\delta = 2 \cdot 10^{-3}$  (left), and with ratio detection,  $\delta = 6 \cdot 10^{-3}$  (right).

P. Hinow, J. Yen, J. R. Strickler. Olfaction in a viscous environment: The "color" of sexual smells in *Temora longicornis*. *Sci. Nat.* **104**:46 (2017)

# Implementation of ratio detection

In moths, the neuroanatomy of the olfactory system is well understood. There are groups of “generalist” and “specialist” neurons that receive input from the olfactory receptor neurons.



A computational network topology of the macroglomerular complex where pointed arrows are excitatory relationships while blunt arrows are inhibitory.

Zavada *et al.* PLoS 1 **6**:e16308 (2011)

# Neuron types

1. olfactory receptor neurons ( $ORN_{a/b}$ ) - respond to chemical binding with compounds  $a$  and  $b$
2. specialist local neurons ( $LN_{a/b}$ ) - receive input from the corresponding ORN type only
3. generalist local neuron ( $LN_{gen}$ ) - receives input from both ORN types

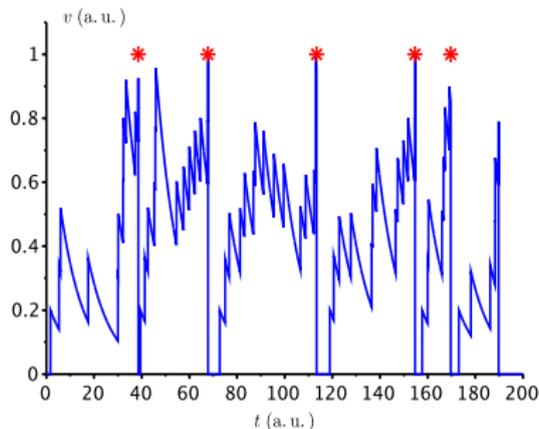
# LIF neuron (Louis Lapicque, 1907)



The membrane potential of the Leaky Integrate-and-Fire neuron is given by

$$\tau \frac{dv}{dt} = -v(t) + RI(t),$$

where  $\tau$  is the membrane time constant,  $R$  is the resistance and  $I$  the external current. Spikes are generated whenever  $v$  reaches a threshold  $\vartheta$ ; then it is reset to the resting potential  $v_r$ .



# Conductance-based synapses, no external currents

As long as no spiking takes place,

$$\tau \frac{dV}{dt} = (V_r - V) + g_{ex}(E_{ex} - V) + g_{inh}(E_{inh} - V),$$
$$\tau_{ex} \frac{dg_{ex}}{dt} = -g_{ex}, \quad \tau_{inh} \frac{dg_{inh}}{dt} = -g_{inh}.$$

Upon spiking of a presynaptic neuron at time  $t$ , all postsynaptic neurons have their excitatory respectively inhibitory conductances changed,

$$g_{ex}(t+) = g_{ex}(t-) + w_{ex}, \quad g_{inh}(t+) = g_{inh}(t-) + w_{inh},$$

depending on the nature of the synapse.

Vogels and Abbott, J. Neurosci. **25**:10786 (2005)

# Parametrization of the ORNs

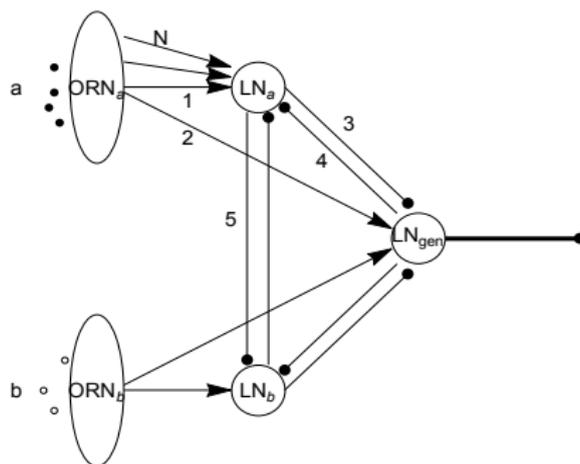
ORNs are modeled as Poisson sources with firing rates  $r_a$  and  $r_b$ , respectively. Each ORN's firing rate grows linearly with respect to the logarithm of the ligand concentration (observations in moths: Kaissling 1996).

Symmetry assumptions for the synaptic weights (target ratio 1:1)

1. the connections  $\text{ORN}_x \rightarrow \text{LN}_x$  have the same weights for  $x = a$  and  $x = b$ ,
2. the connections  $\text{ORN}_x \rightarrow \text{LN}_{gen}$  have the same weights for  $x = a$  and  $x = b$ ,
3. the mutual inhibition between  $\text{LN}_a$  and  $\text{LN}_b$  is symmetric,
4.  $\text{LN}_{a/b}$  act the same way on  $\text{LN}_{gen}$ , and
5.  $\text{LN}_{gen}$  acts the same way on  $\text{LN}_{a/b}$ .

Thus there are five independent weights.

# The network once more



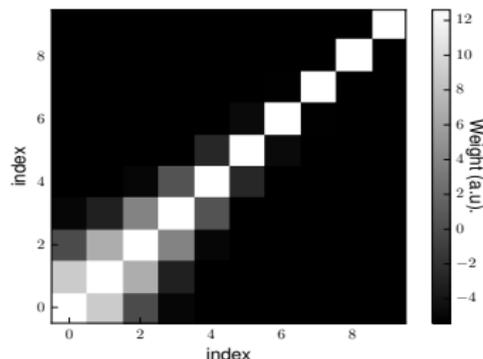
The output of the generalist neuron  $LN_{gen}$ , *i.e.* its firing rate  $r_{gen}$  is the output of the mechanism, as a function of the firing rates  $r_a$  and  $r_b$  of the ORNs. This gives a “response matrix”  $\mathbf{R}$ .

# Synaptic weight selection

For every weight vector we define its cost as

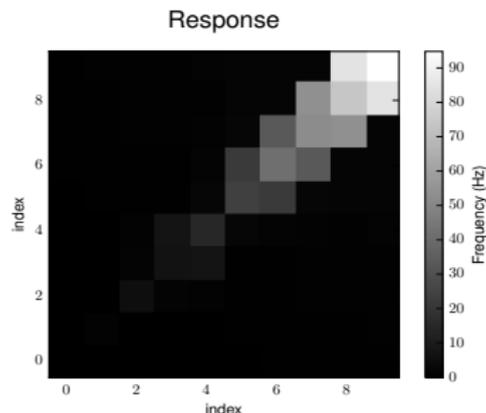
$$C_{\mathbf{T}}(\mathbf{w}) = - \sum_{i,j=1}^{10} R_{i,j} T_{i,j},$$

where the convolution kernel  $\mathbf{T}$  is given by



We implement a Simulated Annealing (SA) algorithm to determine the optimal weights.

Connection	Weight ( $\mu\text{S}$ )
$\text{ORN}_{a/b} \rightarrow \text{LN}_{a/b}$	0.14025 ( $w_{ex}$ )
$\text{ORN}_{a/b} \rightarrow \text{LN}_{gen}$	0.06980 ( $w_{ex}$ )
$\text{LN}_{a/b} \rightarrow \text{LN}_{b/a}$	0.77945 ( $w_{inh}$ )
$\text{LN}_{a/b} \rightarrow \text{LN}_{gen}$	0.64391 ( $w_{inh}$ )
$\text{LN}_{gen} \rightarrow \text{LN}_{a/b}$	0.59438 ( $w_{inh}$ )



1. excitatory connections from the ORNs to the specialist LNs are stronger than to the generalist LN
2. mutual inhibition relations between the local neurons are of similar strength

W. Langhoff *et al.*, Chemosensation and Potential Neuronal Mechanism of Ratio Detection in a Copepod, In: "Trends in Copepod Studies - Distribution, Biology and Ecology", M. Uttieri (ed.), Nova Science Publishers, 14 p. (2017)

# Summary

- ▶ A searching agent that is capable to detect a ratio outperforms a searcher that depends on the gradient of a single compound.
- ▶ Even a minimalistic, simplified neuronal model is capable of ratio detection.

# Putting the sciences together

Future research needs to elucidate

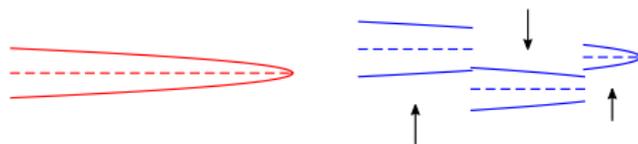
1. the chemical structure and properties of the odorants in the pheromone blend (analytical chemistry),
2. the integration of the pheromone ratio and other signals, e.g. hydromechanical signals, resulting in mate tracking behavior (computational neuroscience),
3. the structure of the copepod brain as well as differences and similarities with other arthropods (neuroanatomy).

# The role of turbulence

The *Kolmogorov length scale* is given by  $\eta = \left(\frac{\nu^3}{\varepsilon}\right)^{\frac{1}{4}}$ , where  $\nu$  is the kinematic viscosity and  $\varepsilon$  is the average rate of dissipation of kinetic energy per unit mass. Below this length the viscosity dominates and energy is dissipated into heat.

A wide range of energy dissipation rates have been reported (calm and stormy days, ocean reliefs, tidal currents etc.). Laboratory experiments are all done in water at complete rest.

**If the trails are torn apart mildly, are they still useful for following?**

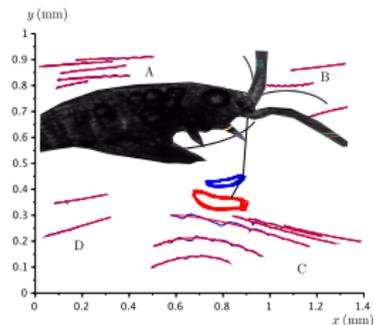
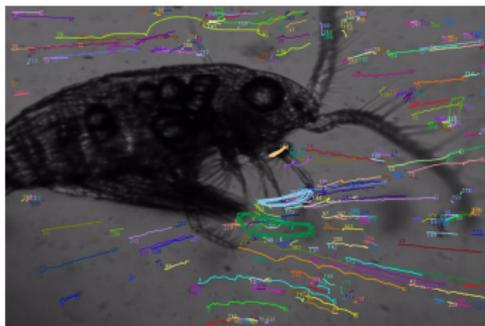


# Near-field feeding currents



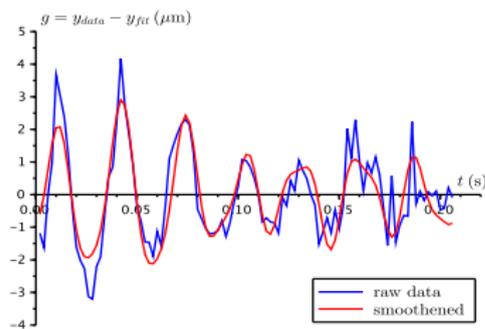
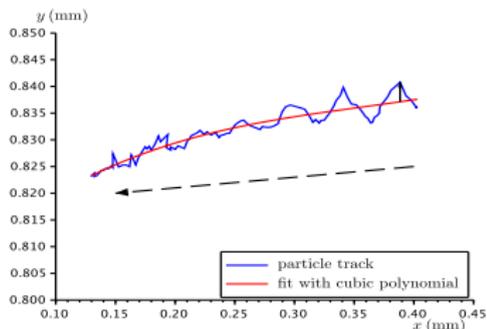
Freely swimming *Leptodiaptomus sicilis*, body length is  $\approx 1$  mm;  
from the Strickler lab.

# Summary of the film



**(Left)** A view of the animal. **(Right)** Traces of the limb joints and selected immersed particles.

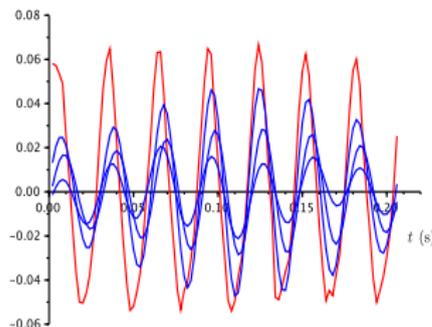
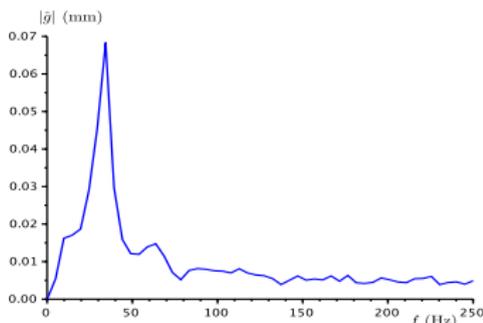
# Fitting the particle trajectories



**(Left)** A sample trajectory of a particle and the optimal fit with a cubic polynomial. **(Right)** The deviations from the centerline.

C. Giuffre *et. al.*, Oscillations in the near-field feeding current of a calanoid copepod are useful for particle sensing, *Sci. Rep.* **9**:17742 (2019)

# Fourier spectra



**(Left)** The averaged Fourier spectra of 15 particle trajectories. The frequency peak is located at  $f = 35$  Hz. **(Right)** Smoothed particle oscillations (blue) and the oscillations of the appendage (red).

C. Giuffre *et. al.*, Oscillations in the near-field feeding current of a calanoid copepod are useful for particle sensing, *Sci. Rep.* **9**:17742 (2019)

# Phase shift between fluid and immersed particles

In an oscillating flow with frequency  $f$  and amplitude  $A$ , the fluid velocity and immersed particle velocity are given by

$$u_f(t) = 2\pi fA \cos(2\pi ft),$$
$$u_p(t) = 2\pi fA\eta \cos(2\pi ft + \beta).$$

where  $\eta$  is the amplitude ratio and  $\beta$  is the phase shift. The key is that algal particles are  $\approx 5\%$  denser than water.

With the particle diameter  $d \ll 1$ , we have  $\text{Re} \approx 0$ , and the “creeping” (or Stokes) flow approximation applies,  $\frac{D}{Dt} \mathbf{u} = 0$ .

R. Clift *et al.*, *Bubbles, Drops and Particles*, Academic Press (1978)

# Rigid sphere in oscillatory motion

We obtain the **Stokes number**  $\tau$ , amplitude ratio  $\eta$  and phase shift  $\beta$

$$\tau = \frac{2\nu}{\pi f d^2}, \quad H_2 = \frac{9}{2\gamma + 1} \sqrt{\frac{\tau}{2}},$$
$$H_1 = \frac{2(1 - \gamma)/(2\gamma + 1)}{H_2^2(1 + \sqrt{2\tau})^2 + (1 + H_2)^2},$$
$$h_1 = H_1(1 + H_2), \quad h_2 = H_1 H_2(1 + 2\tau),$$
$$\beta = \arctan \frac{h_2}{1 + h_1}, \quad \eta = \sqrt{(1 + h_1)^2 + h_2^2}$$

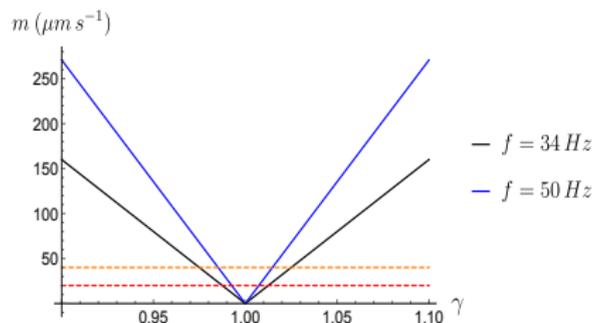
Molerus, *Chem. Ing. Tech.* **36** (1964)

Hjelmfelt & Mockros, *Appl. Sci. Res.* **16** (1966)

# Maximum relative velocity

The maximum relative velocity between the particle and the local water motion is

$$m := \max(u_p(t) - u_f(t)) = 2\pi fA\sqrt{\eta^2 - 2\eta \cos \beta + 1}.$$



Maximal velocity difference at the particle location as a function of the density ratio  $\gamma$  with two possible detection thresholds.

C. Giuffrè *et. al.*, Oscillations in the near-field feeding current of a calanoid copepod are useful for particle sensing, *Sci. Rep.* **9**:17742 (2019)

# Does the signal reach back?



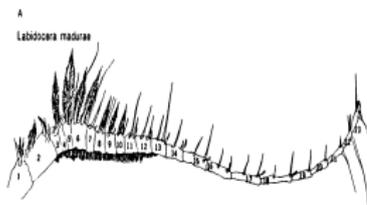
The thickness of the Stokes boundary layer is given by  $\delta = \sqrt{\frac{2\nu}{\omega}}$ .

L.D. Landau, E.M. Lifshitz, *Fluid Mechanics*, Pergamon Press (1987)

# Can the copepod “hear” the difference?

The maximum relative velocity between the particle and the local water motion is  $160 \mu\text{ms}^{-1}$ . The damping distance to  $e^{-1}$  ( $\approx 37\%$ ) is  $240 \mu\text{m}$ . So we would still have a signal of  **$60 \mu\text{ms}^{-1}$** .

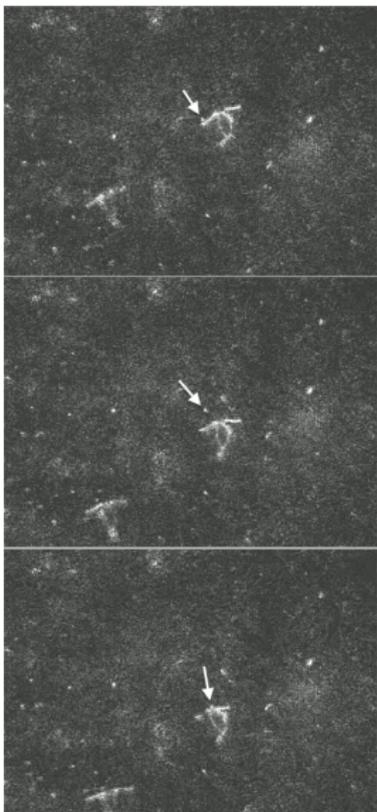
Is that small? Yes, but we are talking about extremely good “ears”.



Setae can react to velocities above  $20 \mu\text{ms}^{-1}$ .

Yen *et al. J. Plankton Res.* **14** (1992); [hawaii.edu/microangela/](http://hawaii.edu/microangela/)

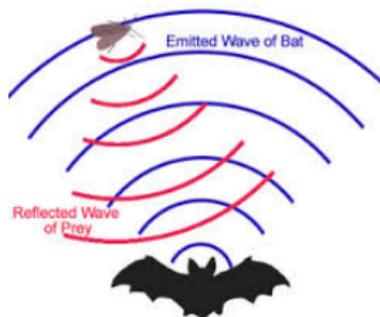
# Further evidence of hydromechanical tracing



Combined dorsal views (central area) and lateral views (lower left corner) of one animal and a particle of interest.

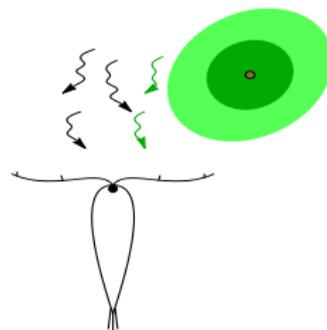
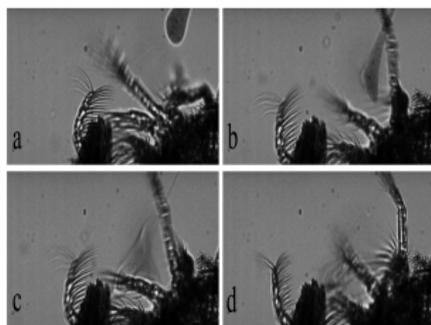
Sense, retract, and capture!

# Summary: Potential echolocation in copepods



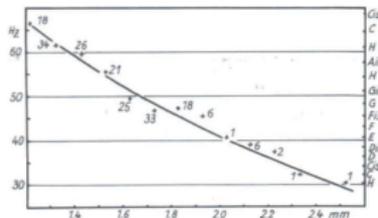
The signal is sent out and the returning signal is strong enough to contain information about an upcoming “algal” particle.

# Possible complementary chemoreception



**(Left)** A feeding copepod *Diaptomus minutus* and an ink droplet that is quickly dispersed (“chaotic advection”). **(Right)** The algal cell is surrounded by a “phycosphere” of leaked chemicals.

# Selected beating frequencies in copepods

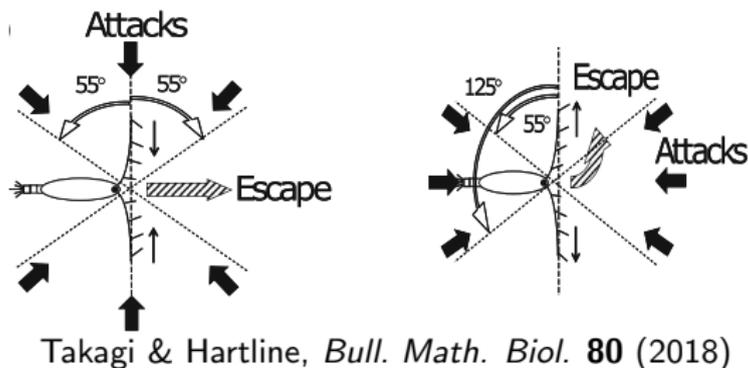


Schröder *Arch. Hydrobiol.* **XXV** (1961)

Beating frequencies of various copepods as function of their body length. How are behaviors encoded in inheritable material?

# Our daily inverse problem

“Hear” the water move, where to?



There are blind spots in the “vision” field of a copepod.

# Acknowledgments

- ▶ Rudi Strickler (UWM), Jeannette Yen (Georgia Institute of Technology), William Langhoff (UWM)
- ▶ Houshuo Jiang (Woods Hole Oceanographic Institution), Carl Giuffre (Adelphi University, New York)
- ▶ Marco Uttieri (Stazione Zoologica “Anton Dohrn”, Naples, Italy)
- ▶ Simons Foundation collaboration grant
- ▶ UWM Support for Undergraduate Research Fellows
- ▶ our reviewers

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Thank you for your attention!