Tiny Giants - Mathematics Looks at Zooplankton

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Georgia Institute of Technology
Atlanta, GA, October 7th, 2016.

Collaborator

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Department of Biological Sciences
University of Wisconsin - Milwaukee

Overview of the talk

- What is plankton, why do we care?
- Near-field feeding current and particle sensing in copepods
- Statistical mechanics of *Daphnia* behavior
- Olfaction in a viscous environment
- Outlook and future research

Before we start, a bit about myself

PhD in Mathematics, Vanderbilt University (2007)

Research interests

- dynamical systems, differential equations, stochastic processes
- applications in biomathematics
  - targeted drug delivery, in particular to the brain
  - microtubule assembly
  - aquatic behavioral ecology (today's topic)
  - tumor growth, angiogenesis, optimization of treatment

If you think I can be of help in your research . . .

My mind is open.

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 - carries out $\approx 70\%$ of all photosynthesis on earth

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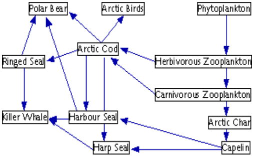
- phytoplankton - carries out $\approx 70\%$ of all photosynthesis on earth
- zooplankton - heterotrophic, provide crucial link in the marine food web



Zooplankton diversity



- Zooplankters have sizes between 1 μm 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).

Copepod diversity and abundance

- 13,000 species of copepods have been described (Boxshall & Defaye, 2008), this number is growing.
- 10^{37} C-atoms are fixed in copepods, possibly the largest amount of biomass in any animal group (Buitenhuis *et al.*, 2006).
- There may be 3.2×10^{21} copepods in the global ocean and other water bodies.

Plankton ecology and emerging dangers

- Anthropogenic global climate change results in shifts of biogeographic boundaries, leading to changes in species distributions.
- Ocean acidification changes growth rates of key phytoplankton species.

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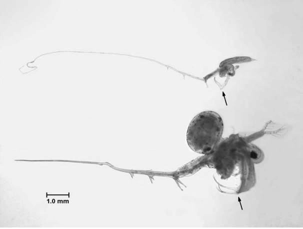
- Ocean acidification changes growth rates of key phytoplankton species.
- Invasive species compete with native species and are less palatable to higher trophic levels.



Cercopagis pengoi, Bythotrephes longimanus; Daphnia lumholtzi

Mathematical modeling approaches

Typically, but not exclusively

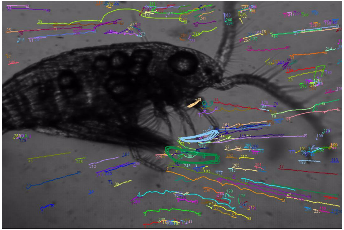
- population dynamics to study nutrient cycles, food web dynamics, parasite infestations
- size and age-structured models (i.e. PDEs)
- individual-based models, simulations
- computational fluid dynamics of individual swimmers, colonies and swarms
- fractal analysis of recorded swimming paths

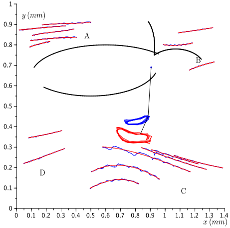
Part I: Near-field feeding currents

Movie

Freely swimming *Leptodiaptomus sicilis*; from the Strickler lab.

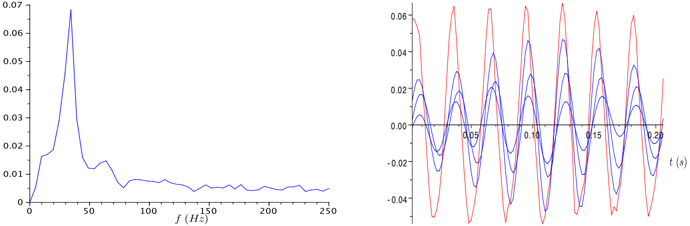
Part I: Summary of the film





The oscillation of the appendage *(left)* and selected traces of immersed algal particle fitted with cubic polynomials *(right)*.

Part I: Fourier spectra



The averaged Fourier spectra of 15 particle trajectories *(left)* and smoothened particle oscillations (blue) and the oscillations of the appendage (red) *(right)*. The frequency peak is located at $f = 35\,Hz$.

Fluid velocity and immersed particle velocity are given by

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

where η and β are the amplitude ratio and phase shift, respectively. Fluid-mechanical calculations lead to $\beta = -0.286^\circ$. The key is that algal particles are about 10% denser than water.

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

Part I: Maximum relative velocity

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

$$\begin{aligned}\max(u_R) &:= \max\left(u_p(t) - u_f(t)\right) \\ &= 2\pi f A \sqrt{\eta^2 - 2\eta\cos\beta + 1} = 160\,\mu m\, s^{-1}.\end{aligned}$$

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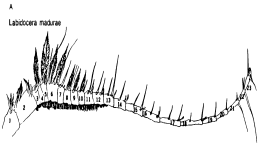
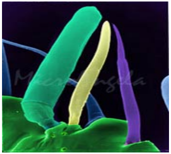
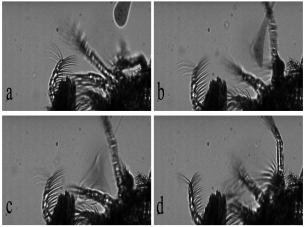
Is that small? Yes, but we are talking about extremely good "ears".





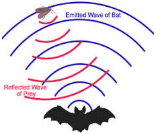
Setae can react to velocities above $20\,\mu m\, s^{-1}$.
J. Yen *et al.* J. Plankton Res. **14**, 1992

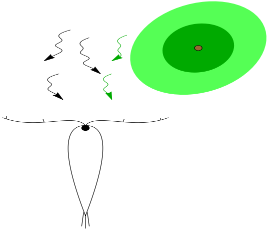


A feeding copepod *Diaptomus minutus* and an ink droplet *(top left)* that is quickly dispersed.

Part I: Animal mechanoreception

Known to occur in spiders, insects, fish, amphibians, mammals etc. If the animal itself is responsible for originating the signal, we speak of echolocation.



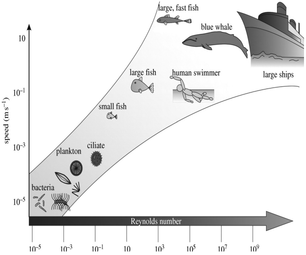


In the copepod, echolocation and chemoreception complement each other in search for edible particles.

P. Hinow, H. Jiang, J. R. Strickler. Near-field feeding current and particle sensing in calanoid copepods. *In preparation*, 2016

$$\mathrm{Re} = \frac{\text{initial forces}}{\text{viscous forces}} = \frac{vL}{\nu},$$

where v is the characteristic velocity, L is the characteristic length, and ν is the kinematic viscosity of the fluid.



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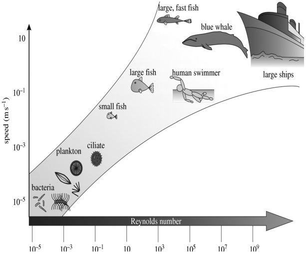
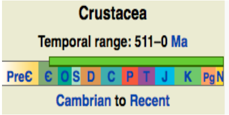


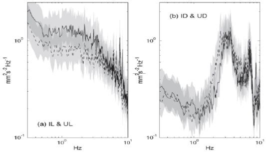


Of course, they've been around for a while.

Part II: Swimming behavior of *Daphnia pulicaria*

Nihongi *et al.* observed *Daphnia pulicaria* under possible infestation with *Vibrio cholerae* and light and dark conditions.

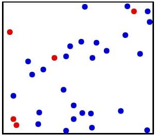
To determine differences in behavior, power spectra of velocity fluctuations and fractal dimensions of paths were used.



A. Nihongi *et al.*, 2011

These characteristics are difficult to define and lack obvious ecological interpretation.

Part II: Statistical mechanics

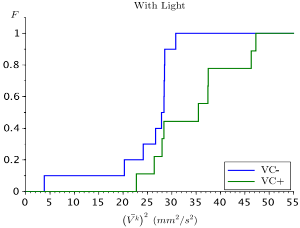


Ludwig Boltzmann (1872): the temperature T of an ideal gas and the average kinetic energy of its particles are related by

$$\frac{1}{2}m\langle v^2\rangle = \frac{3}{2}k_B T,$$

where k_B is Boltzmann's constant.

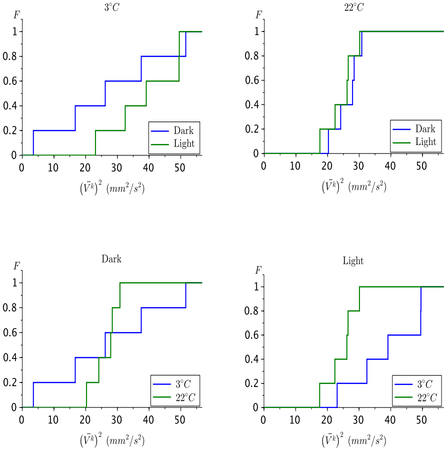
We use the particle analogy to define the "ecological temperature" of the swimmers.



The cumulative distribution functions of ten infested (red) respectively nine uninfested (blue) *D. pulicaria* in presence of light. Statistical testing shows that the difference is significant.

Part II: "Ecological temperature" of *D. pulicaria*

Similar results in warm and cold water.



The ecological temperature is a good discriminator of behavioral differences.

Part II: Why these changes?

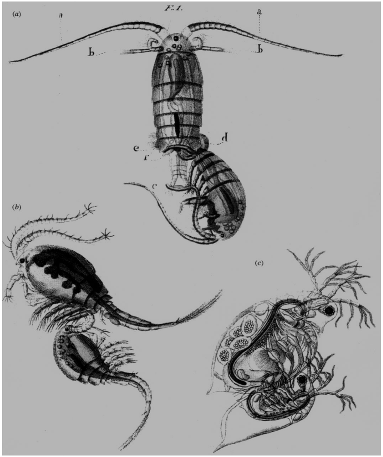
V. cholerae adheres to the chitin exoskeleton of zooplanktons. Behavioral changes may result in

- increased detection by visual predators such as fish,
- parasite enters the aquatic food chain and so improves its dispersal,
- infested *D. pulicaria* are eliminated from the population and so reduce the chance of other individuals becoming infested.

Behavioral changes due to infections with pathogens are well-documented in many species.

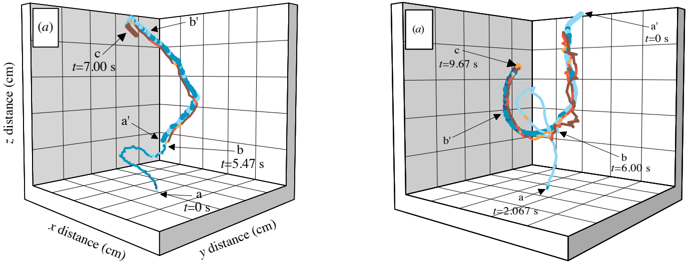
P. Hinow, A. Nihongi, J. R. Strickler. Statistical mechanics of zooplankton. *PLoS One* **10**:e0135258, 2015

Part III: Sex in the deep sea



L. Jurine, *Histoire de Monocles*, Geneva, 1820

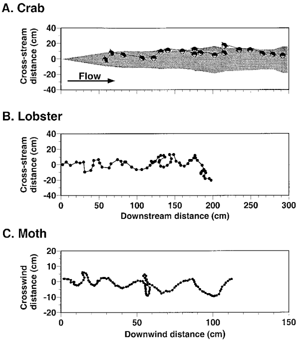
It is dark, the dimensions are three, the mate is hundreds of body lengths away.



Schlieren photography to visualizes trails of females and males. "Fat" trail = female, "thin" trail = male; red and brown colors indicate higher swimming speeds.

M. Doall *et al.* Phil. Trans. R. Soc. Lond. B **353**, 1998; J. Yen *et al.* (2003)

Part III: Olfaction in (semi-)turbulent environments

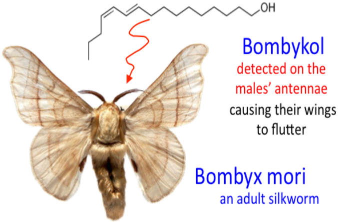


N. J. Vickers, Biol. Bull. **198**, 2000

Chemical sensing is used by animals to find food and mates, to escape dangers, to form colonies etc.

Part III: Pheromones

φέρω - "to bear", όρμή - "impetus"

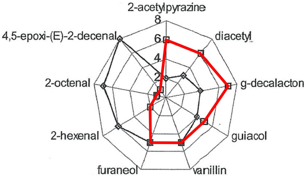


A. Butenandt *et al.* H-S. Z. Physiol. Chem. **324**, 1959

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

Part III: 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".



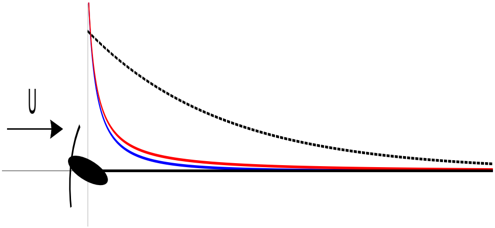
W. Grab, Givaudan S.A., Switzerland

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

Part III: Building the trail

The female is moving with constant velocity U, and produces compounds at rate Q that have diffusion and decay rates D and k_i, respectively (same production and diffusion rates). Then the concentration of compound i along the trail is given by (to good approximation)

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



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

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 μ steps, which is a Poisson-distributed random variable.

Part III: 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,

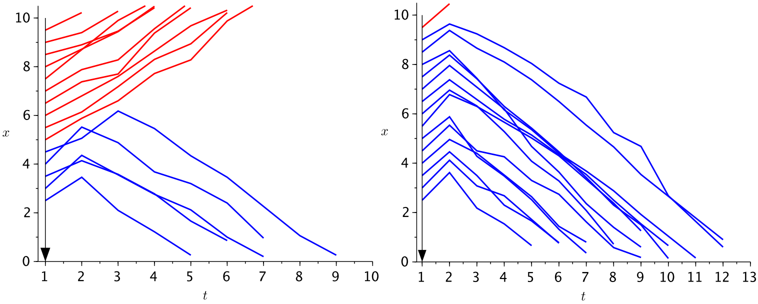
$$u_1(x) = \frac{1}{10x} \exp\left(-\frac{x}{20}\right), \quad u_2(x) = \frac{1}{10x} \exp\left(-\frac{x}{10}\right).$$

and the male can detect the ratio

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

The initial direction of the male is always set to "wrong".

Part III: Increased success rate for ratio detection

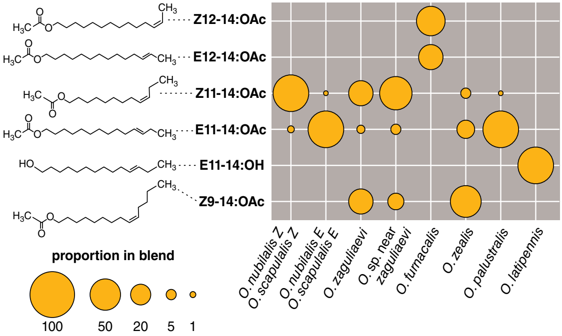


Successful (blue) and unsuccessful (red) searches with single compound, $\delta = 2 \cdot 10^{-3}$ *(left)*, and with ratio detection, $\delta = 6 \cdot 10^{-3}$ *(right)*.

P. Hinow, J. Yen, J. R. Strickler. Olfaction in a viscous environment: Calanoid copepods as models. *In preparation*, 2016

Part III: Other reasons for “blended” pheromones

Individuals detect conspecifics from the composition of the pheromone blend.



Different compounds in pheromones of *Ostrinia* moths.

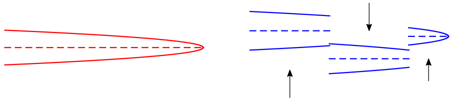
J.-M. Lassance *et al.*, Proc. Natl. Acad. Sci. USA **110**, 2013

Ongoing and future work: the role of turbulence

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

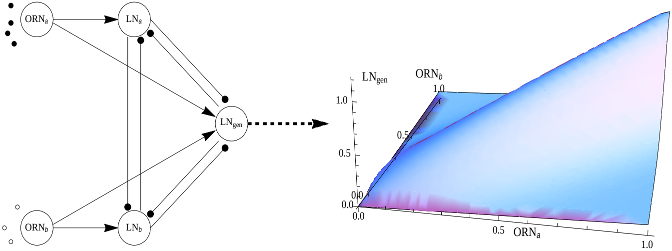
The problem is, a wide range of energy dissipation rates have been reported (calm and stormy days, ocean reliefs, tidal currents etc.). Laboratory experiments are, of course, all done in water at complete rest.

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



Ongoing and future work: the 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.



(Left) The topology of the macroglomerular complex following Zavada *et al.* PLoS 1, 2011. Pointed arrows are excitatory relationships while blunt arrows are inhibitory. *(Right)* The schematic output function of the network for a target ratio of 1 : 1 of compounds *a* and *b*.

Ongoing and future work: putting the sciences together

Future research needs to elucidate

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

Acknowledgments

- Rudi Strickler, Ai Nihongi (UWM), Houshuo Jiang (Woods Hole Oceanographic Institution), Jeannette Yen (Georgia Institute of Technology)
- Simons Foundation collaboration grant

Thank you for your attention!