Toward a mechanistic understanding of the jumping behavior of copepods

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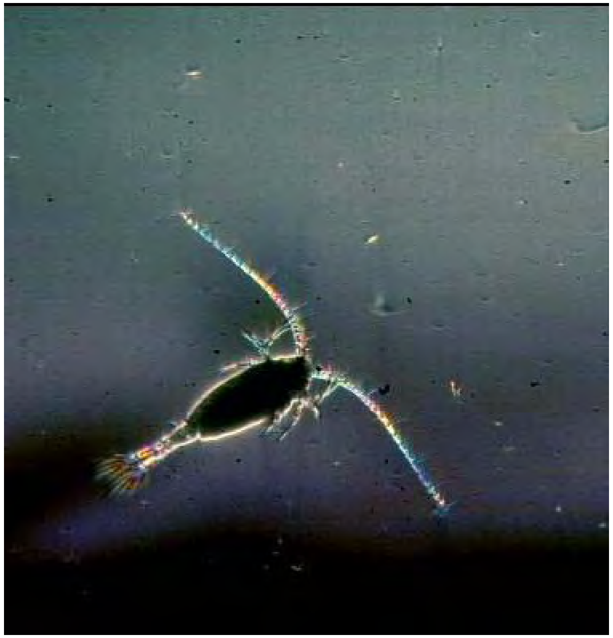
Jumping is a widespread behavior in copepods and serves for multiple purposes.

(1) Jumping for repositioning



Schlieren observation of the calanoid copepod *Limnocalanus macrurus* (2.4-2.9 mm in length) repositioning by jumping (***100 times slower than real time***).

Schlieren observation of two calanoid copepods *Diaptomus minutus* (~1.0 mm in prosome length) jumping to avoid bumping into each other (***in real time***).

Note the distinct mushroom-like vortical flow structures left behind!

Courtesy of Prof. J. Rudi Strickler

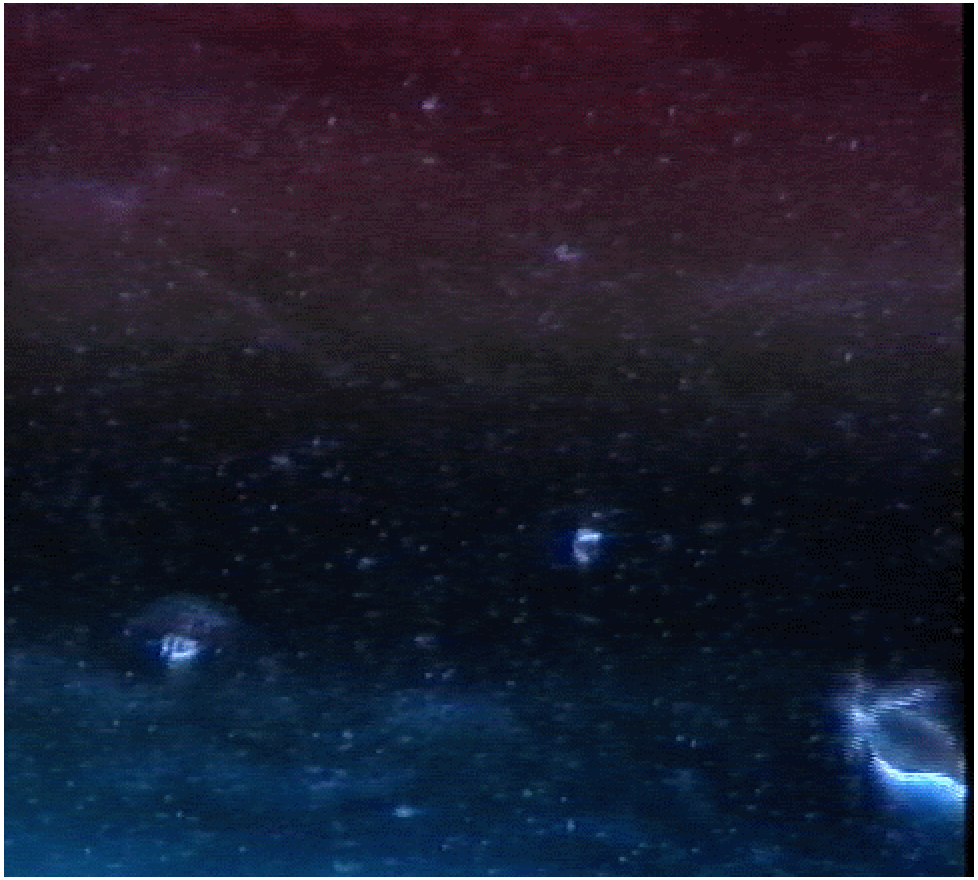
(2) Jumping for swimming around

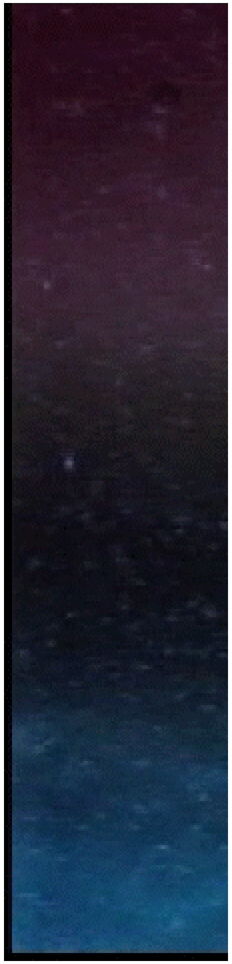
Schlieren observations of the cyclopoid copepod *Cyclops* spp. swimming by jumping;

Body length: 0.5 – 3.0 mm;

Average traveling speed: 1.0 – 5.0 mm/s.

Distinct mushroom-like vortical flow structures were left behind (Strickler 1975).





Courtesy of Prof. J. Rudi Strickler

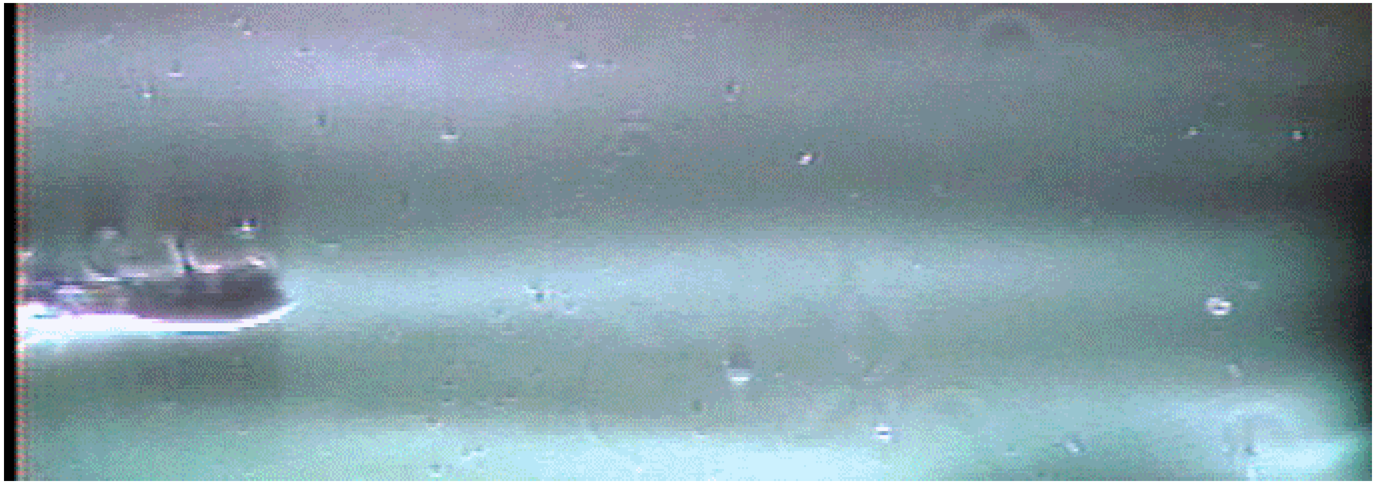
(3) Jumping for attacking prey

Video observation of an *Oithona plumifera* female copepod (~1.0 mm in prosome length) jumping to capture a ciliate prey.

***6 times slower than real time*.**

Jiang & Paffenhöfer (2008)

(4) Jumping for escaping from danger



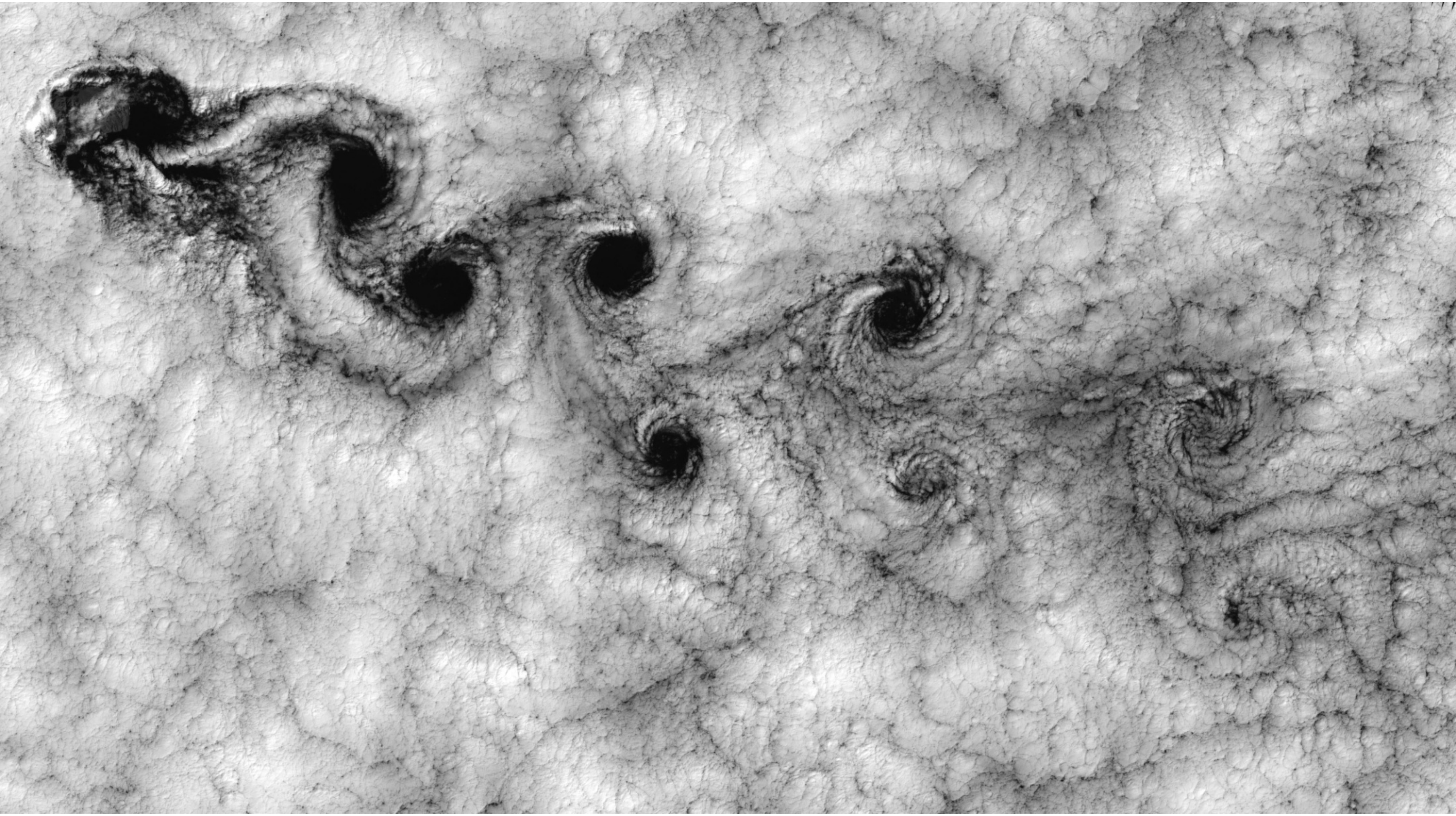
The female copepod *Euchaeta rimana* (~2.4 mm in prosome length) executed a series of escape jumps. Three toroidal flow structures were left behind.

Maximum copepod speed ~ 380 mm/s.

***2.4 times slower than real time*.**

Yen & Strickler (1996)

However, the underlying mechanism is NOT near inviscid vortex shedding due to flow separation!



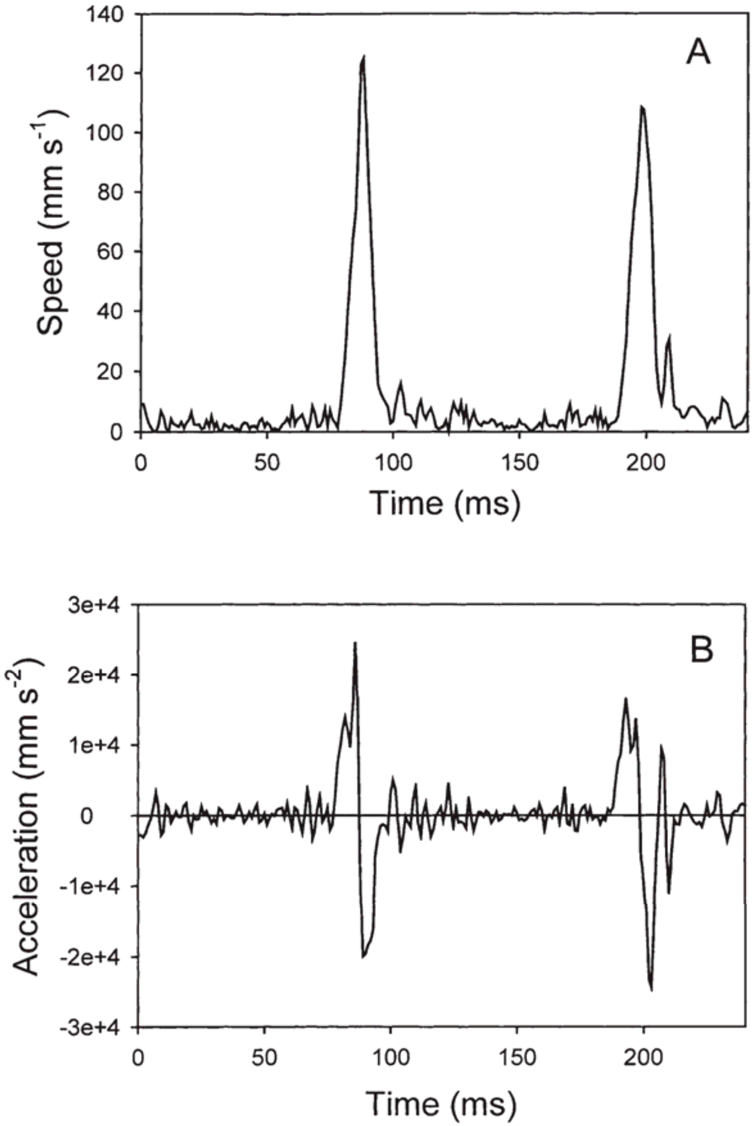
Is jumping energetically more costly or hydrodynamically more dangerous (i.e. more easily detectable by rheotactic predators) than other widespread behaviors such as creating a feeding current or cruising?

To answer these questions, we use:

(1) theoretical hydrodynamic modeling,
(2) particle image velocimetry (PIV), and
(3) empirical data-driven computational fluid dynamics (CFD) simulations

to investigate the jump-imposed water flows.

Key characteristic of copepod jumps: ***Impulsiveness*** (1)

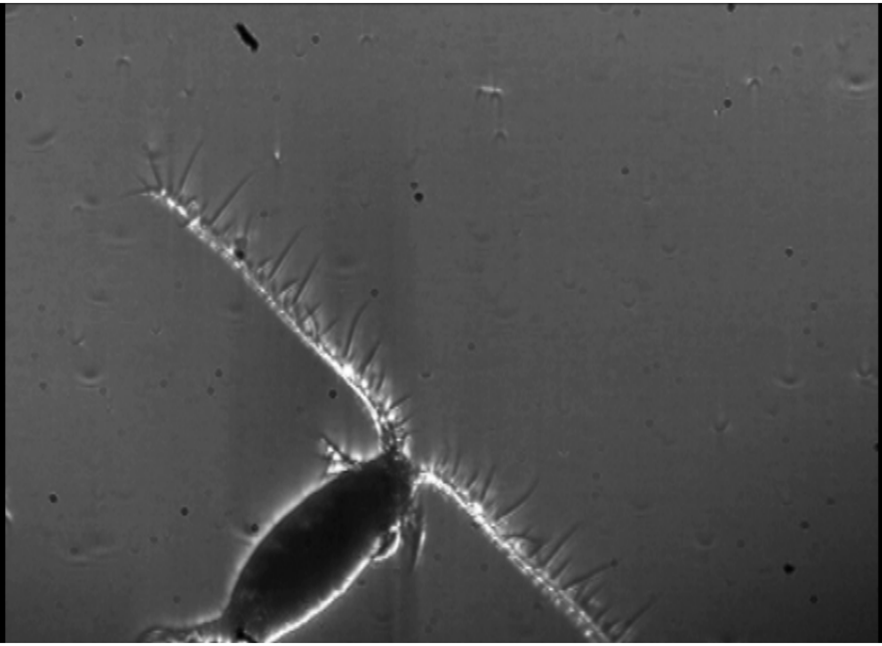


Example of (A) speed and (B) acceleration records for 2 representative spontaneous 'hops' of adult male *Acartia tonsa*.

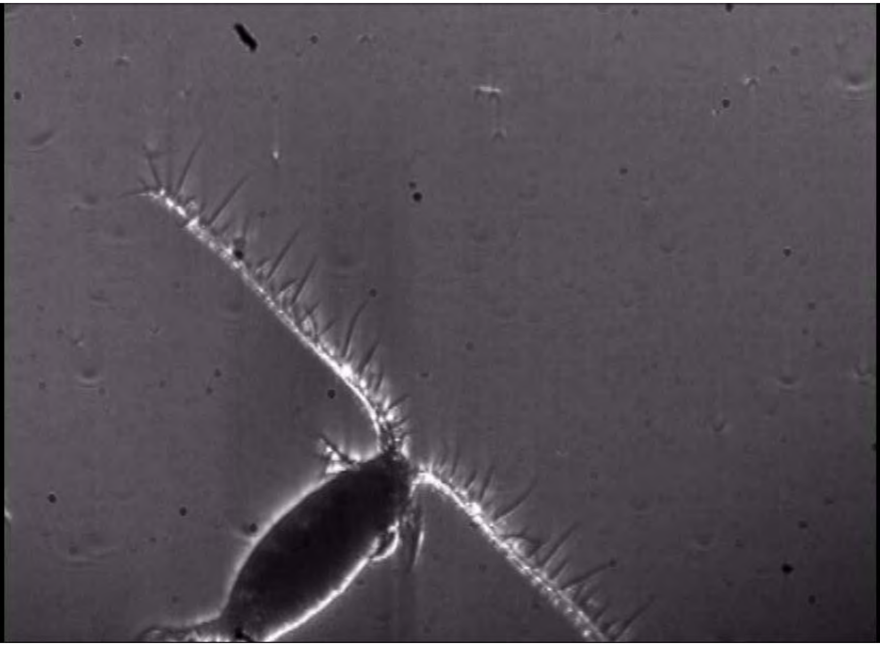
1000 frames s^{-1} high speed video observations (Buskey, E.J., Lenz, P.H. and Hartline, D.K. 2002, *MEPS* 235:135-146).

Key characteristic of copepod jumps: ***Impulsiveness*** (2)

Repositioning by jumping of the copepod *Limnocalanus macrurus* (2.4-2.9 mm in length)



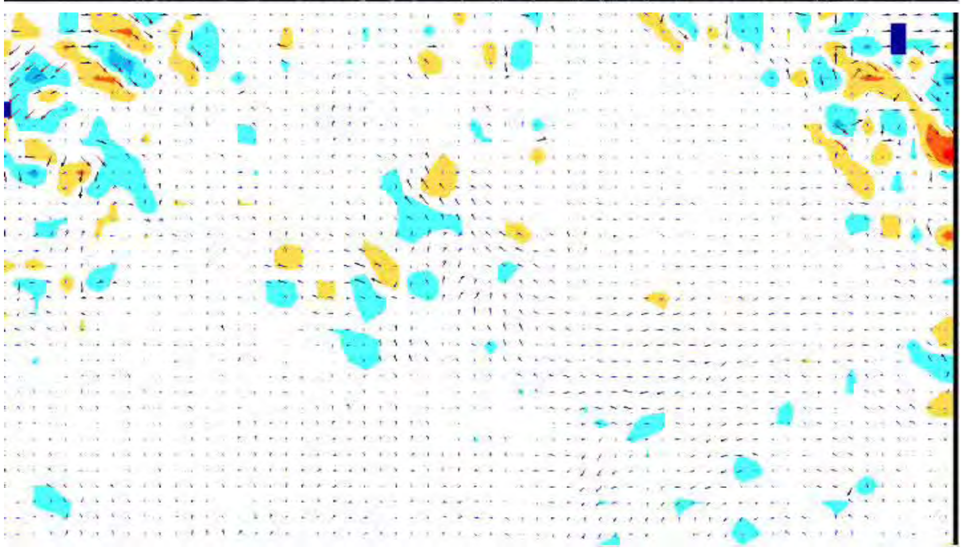
100 times slower than real time



Real time

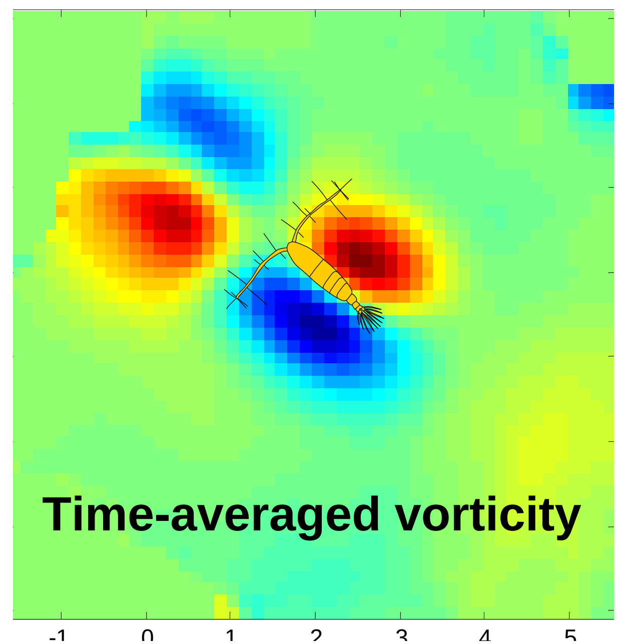
Courtesy of Prof. J. Rudi Strickler

Key characteristic of jump-imposed flow: ***Viscous decay***



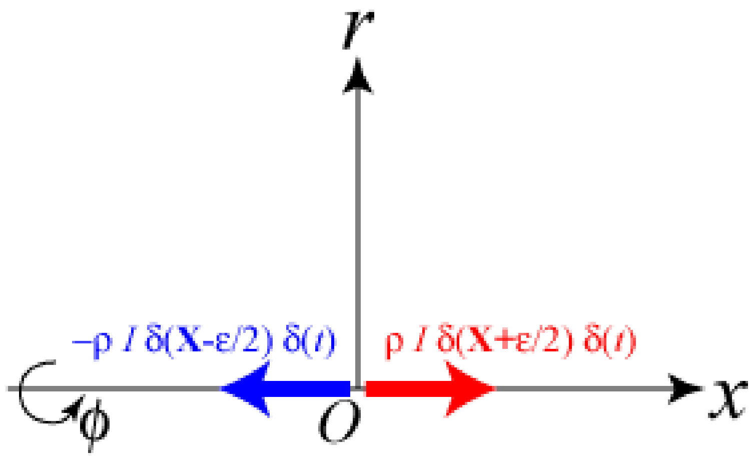
Repositioning Jumps

Re ≡ Γ/ν ~ 2-30



Kiørboe, T., Jiang, H. and Colin, S. P. (2010) Danger of zooplankton feeding: the fluid signal generated by ambush-feeding copepods. *Proceedings of the Royal Society B*, 277, 3229-3237.

Viscous vortex ring model for copepod jumping flow: The impulsive stresslet model



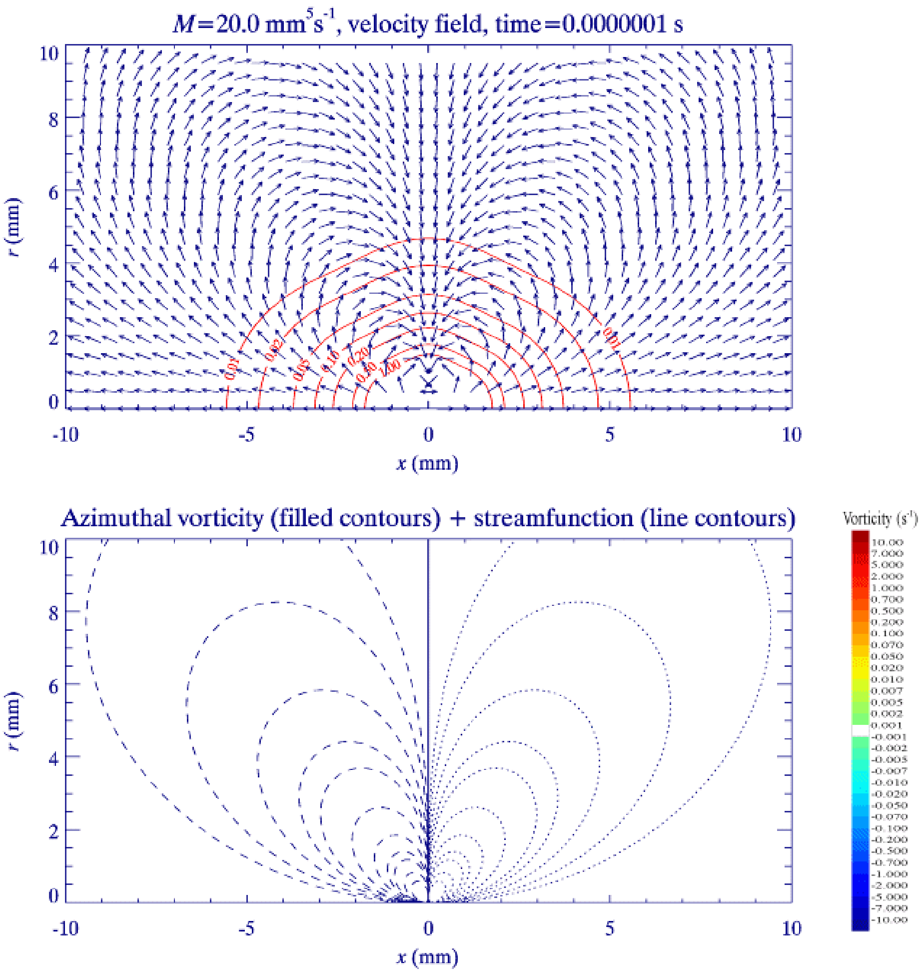
Vorticity (ω_ϕ) and streamfunction (ψ_ϕ) obtained in Stokes approximation:

$$\omega_\phi = \frac{M\,x\,r}{32\,\pi^{3/2}\,(\nu t)^{7/2}}\,e^{-\xi^2}$$

$$\psi_\phi = -\frac{3\,M\,x\,r^2}{2\,\pi^{3/2}\,(x^2+r^2)^{5/2}}\left[-\frac{\sqrt{\pi}}{2}\mathrm{erf}(\xi) + \xi e^{-\xi^2}\left(1+\frac{2}{3}\xi^2\right)\right]$$

where ν the kinematic viscosity, $\xi = \sqrt{\frac{x^2+r^2}{4\nu t}}$ and $\mathrm{erf}(\xi) = \frac{2}{\sqrt{\pi}}\int_0^\xi e^{-y^2}\,dy$

Strength of the impulsive stresslet: $M = \lim_{\varepsilon\to 0, I\to\infty} I\varepsilon = constant$ with $[M] = L^5T^{-1}$.



Two counter-rotating viscous vortex rings of same intensity

(1) At small time the flow far field (i.e. $\xi >> 1$) is approximately irrotational and behaves as:

$$u = \frac{3M}{4\pi}\frac{x(2x^2-3r^2)}{(x^2+r^2)^{7/2}}$$

$$v = \frac{3M}{4\pi}\frac{r(4x^2-r^2)}{(x^2+r^2)^{7/2}}$$

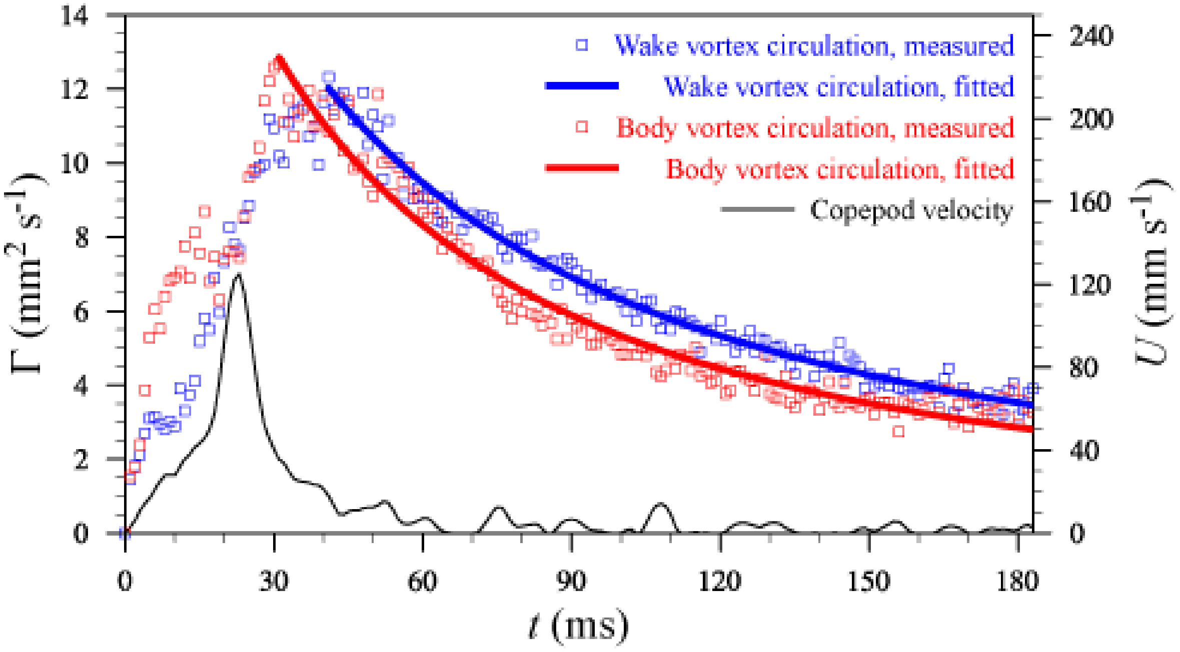
$\sim 1/R^4$

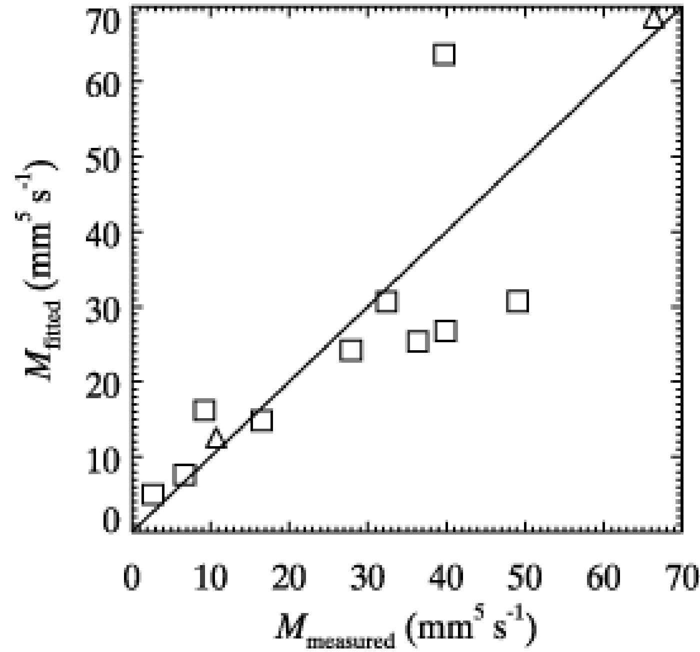
(2) Viscous decay of circulation of the one-signed vorticity:

$$\Gamma_{x\geq 0}(t) \equiv \int_0^{+\infty}\int_0^{+\infty} \omega_\phi \, dx \, dr = \frac{M}{8\pi^{3/2}(\nu t)^{3/2}}$$

Jiang, H. and Kiørboe, T. (2011a) The fluid dynamics of swimming by jumping in copepods. *Journal of the Royal Society Interface*, doi:10.1098/rsif.2010.0481.

Applying the impulsive stresslet model to the PIV flow data





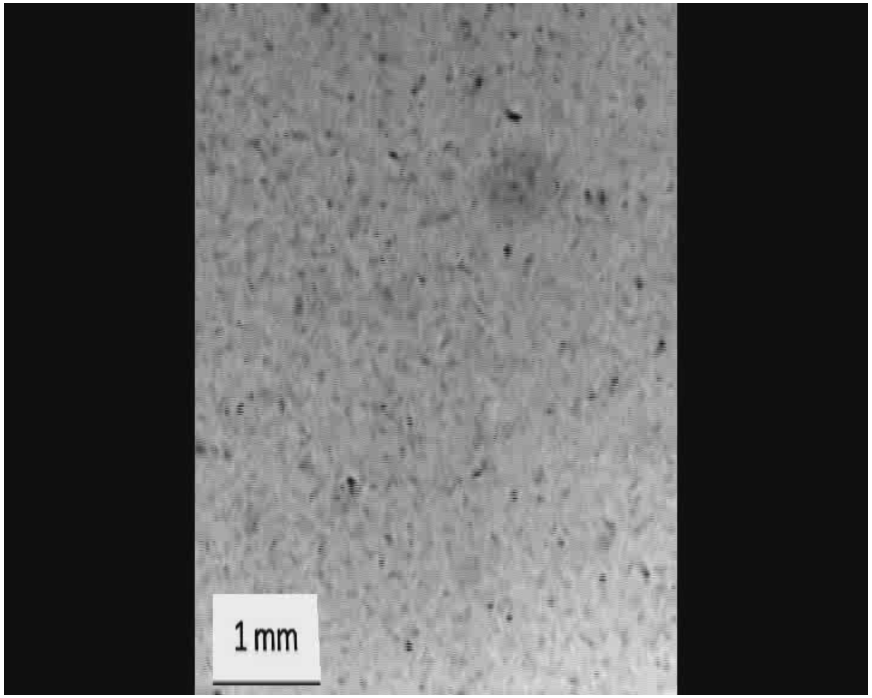
$$M = U_{\max} \times V_{\text{copepod}} \times D_{\text{jump}}$$

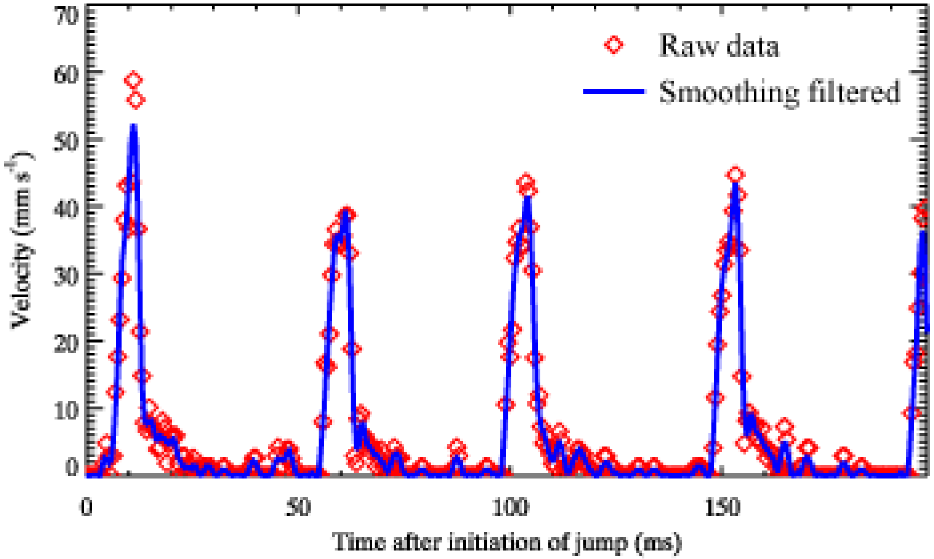
$U_{\max}$: maximum speed attained by the copepod;

V_{copepod}: copepod body volume;

D_{jump}: maximum distance traveled by the copepod during a jump.

Using the impulsive stresslet model to understand the fluid dynamics of swimming by jumping in copepods

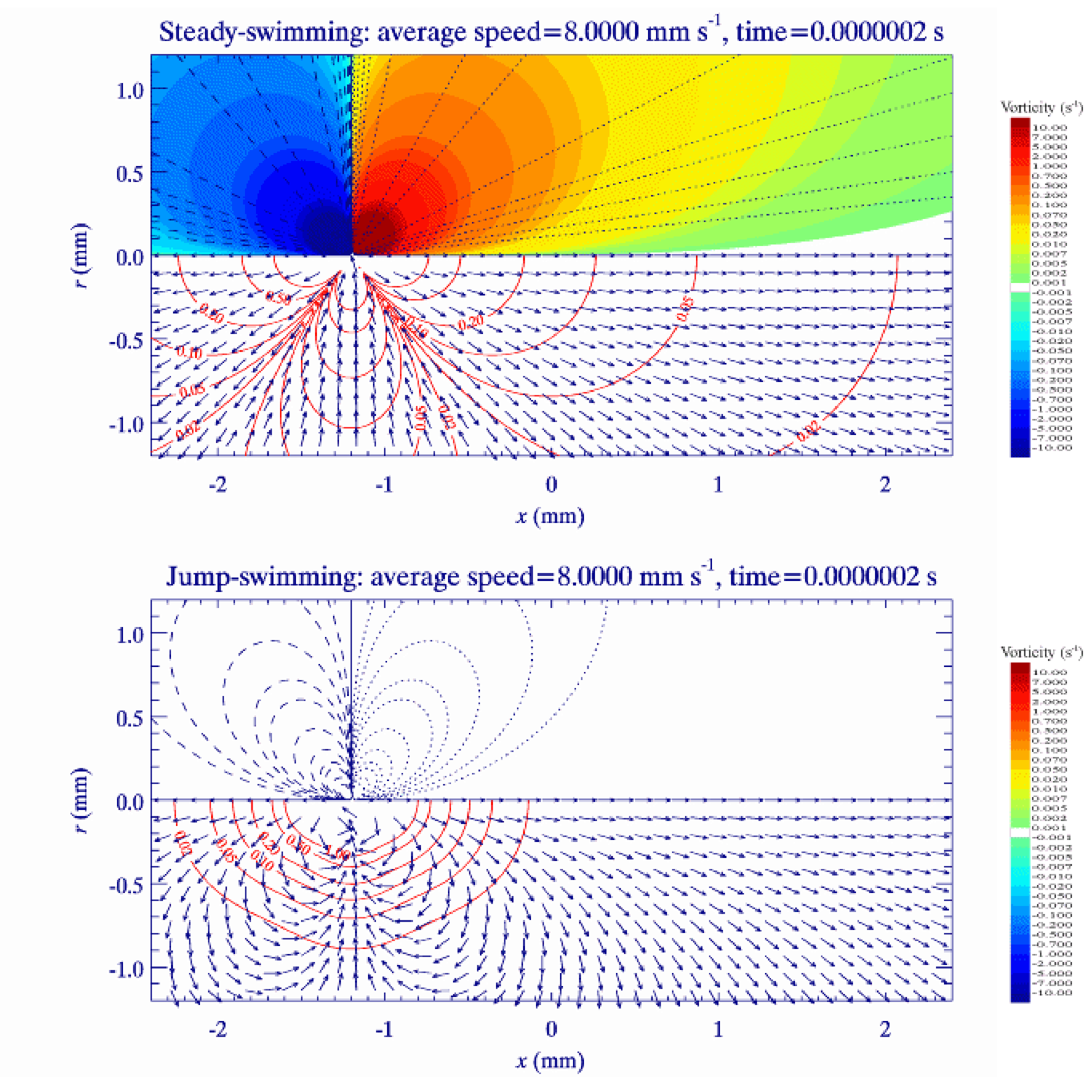


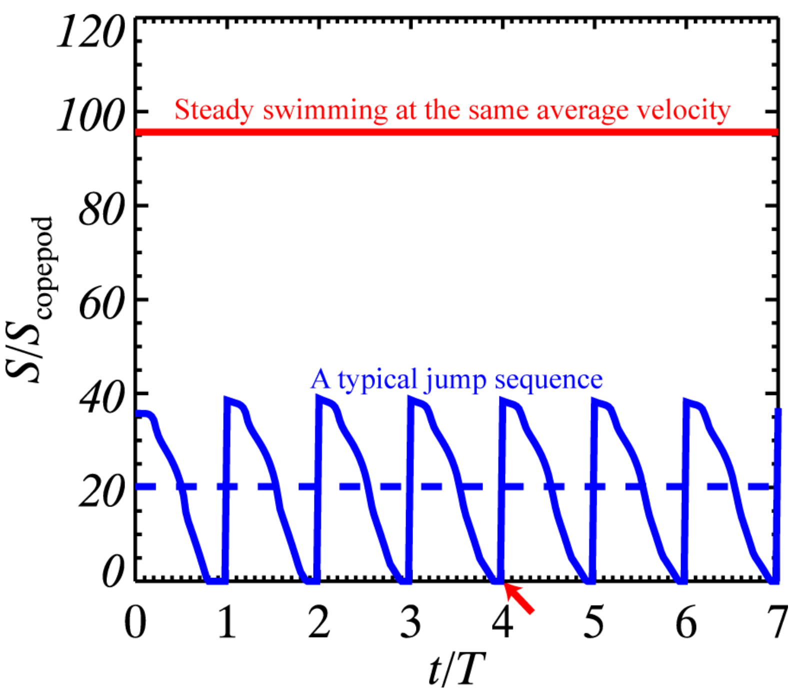


Swimming by jumping in the copepod *Oithona davisae* male:

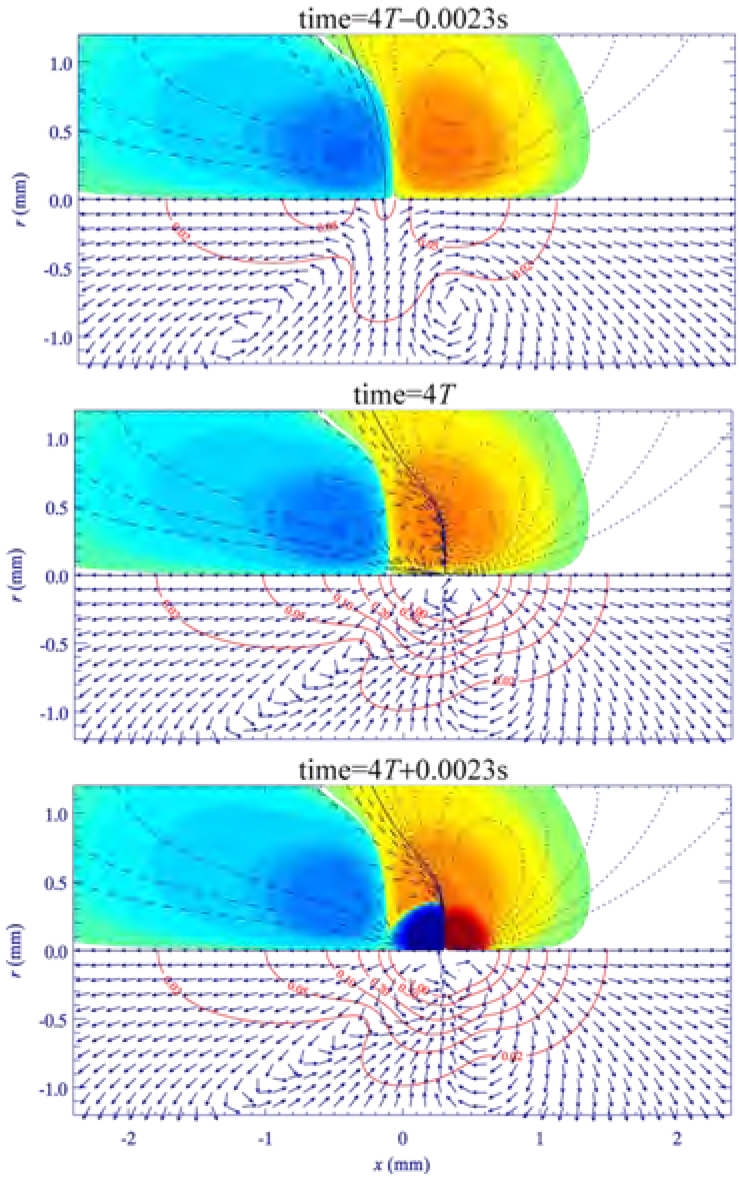
- Prosome length (PL) = 0.3 mm, aspect ratio = 0.5;
- Averaged jump frequency = 21.5 Hz;
- Averaged peak velocity (U_{max}) = 40 mm/s;
- Averaged jump distance (D_{jump}) = 0.375 mm (= 1.25 PL);
- Averaged traveling speed = 8 mm/s.

Swimming by jumping in the male copepod *Oithona davisae* is much quieter than swimming smoothly, provided the two situations have the same averaged traveling speed.





Swimming by jumping in the male copepod *Oithona davisae*: Jump distance ≈ Traveling distance of the body vortex ring



Traveling distance of the body vortex ring within one jump interval:

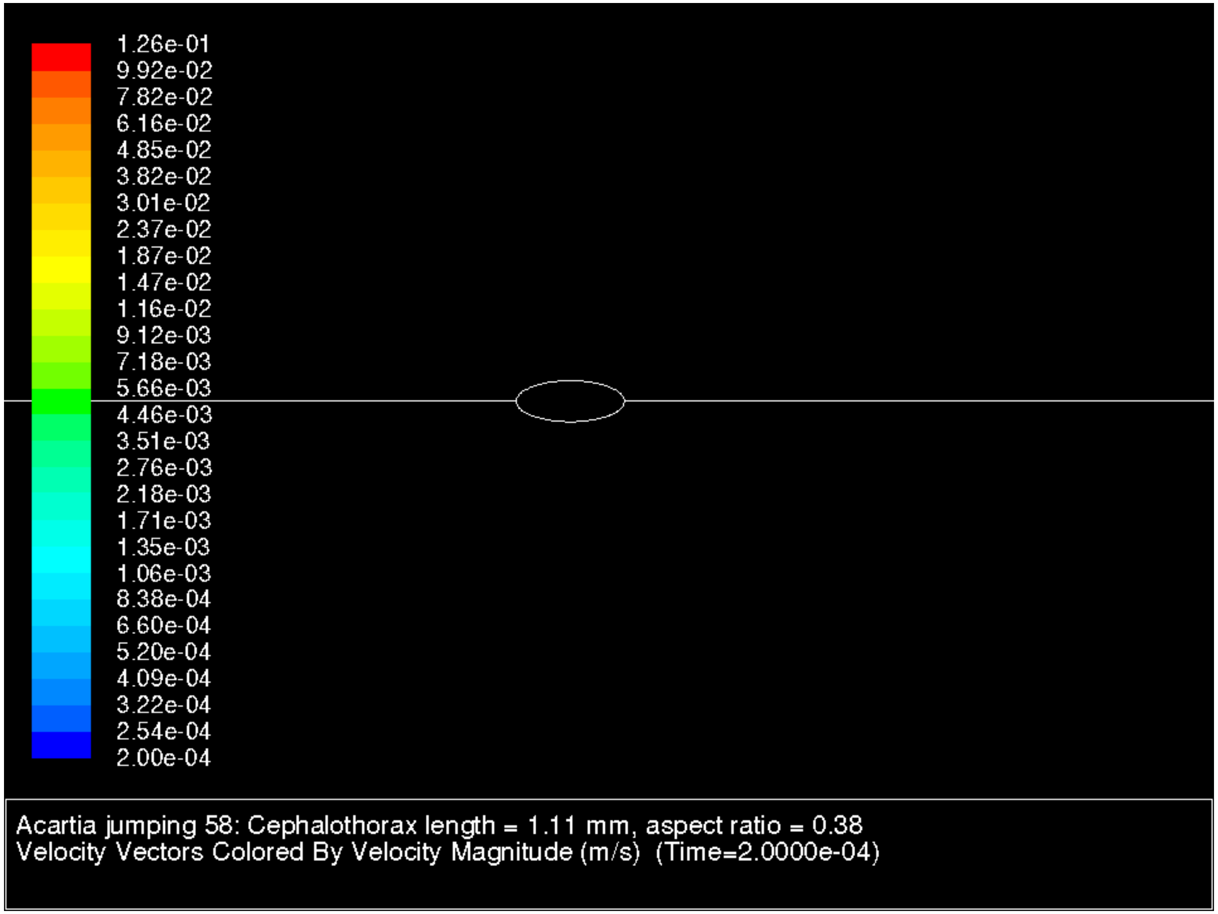
$$\Delta x_{\omega} = \sqrt{2\ \nu T} \sim 0.354\, mm$$

very close to the averaged jump distance, 0.375 mm.

The "stepping stones" analogy

By doing so, all the vortex ring pairs would be regularly distanced and not deformed much from its canonical form (analogy to a train of stepping stones one by one, one disappears and the other emerges).

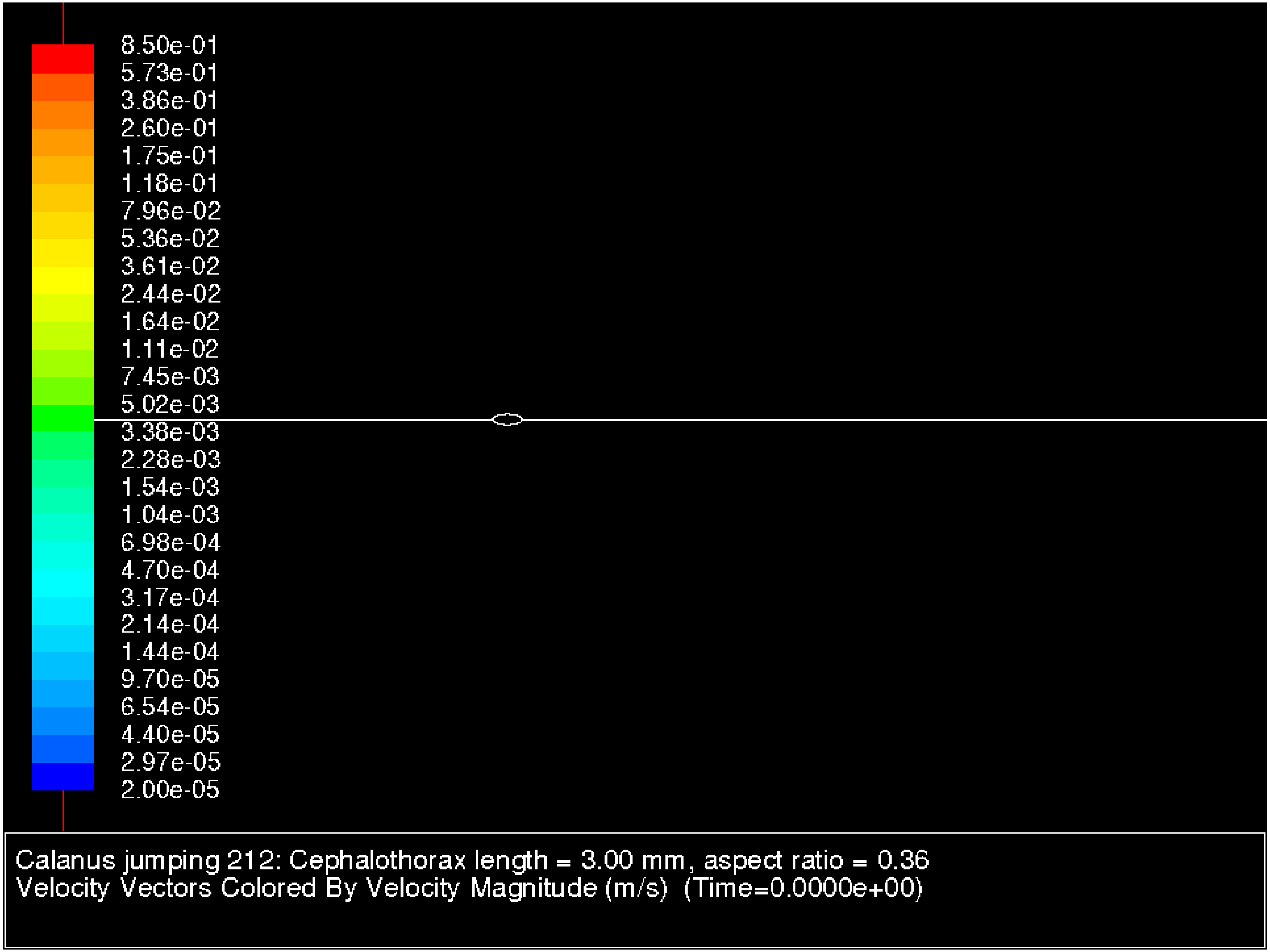
Hypothesis: Creating viscous vortex rings for hydrodynamic camouflage



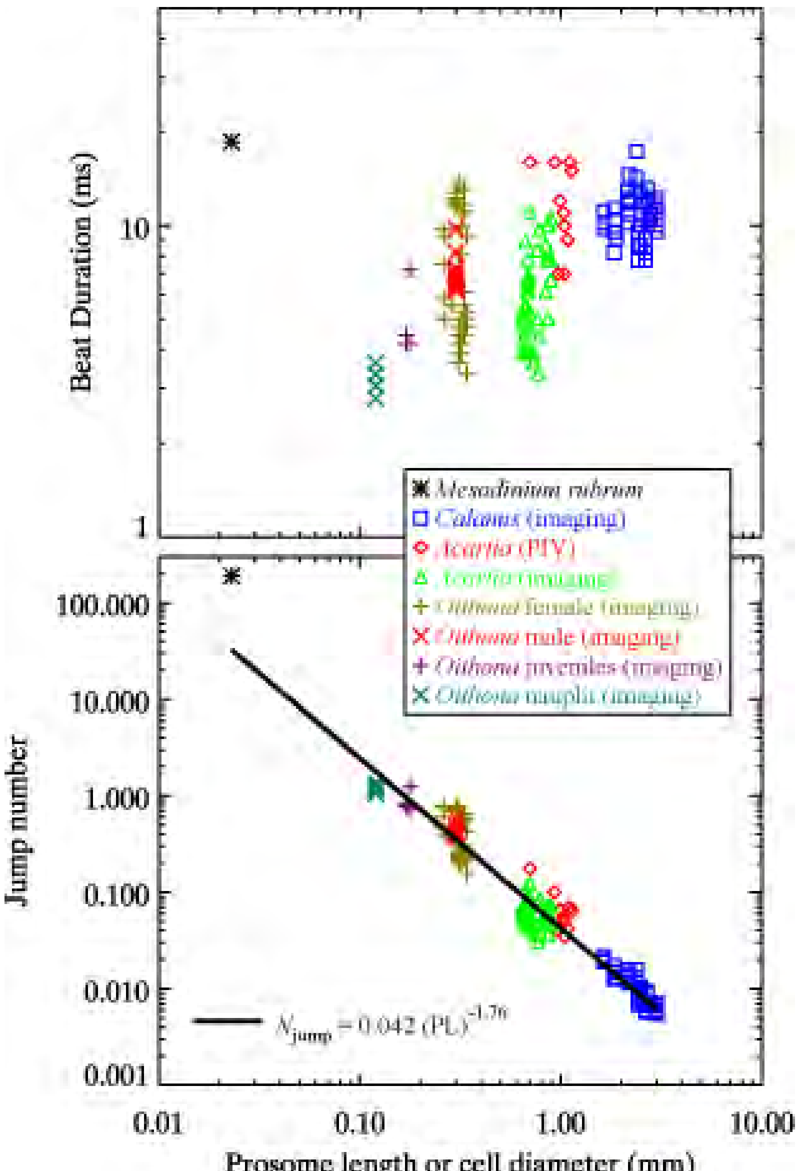
CFD-simulated flow field imposed by **a repositioning-by-jumping copepod** (Jiang & Kiørboe, 2011b, *JEB* **214**:476-486).

The background flow field is likely to be made up of many such viscous vortices, because any unbounded flow that has net linear momentum (or momentum pair) eventually decays to the unique vortex ring solutions of the Stokes equations (Phillips 1956; Shariff & Leonard 1992).

CFD-simulated flow field imposed by <u>a fast escaping copepod</u>



Jet or vortex: the non-dimensional jump number



$$N_{\text{jump}} \equiv \frac{\tau}{L^2/(4\nu)}$$

τ : beat duration of the power stroke;
L : prosome length;
ν : kinematic viscosity.

N_{jump} < ~1 indicates that the jump is impulsive enough to create viscous vortex rings.

SHORT SUMMARY

- **Spatial decay: $1/r^4$ (impulsive stresslet) vs. $1/r^2$ (stresslet);**
  $1/r^3$ (impulsive Stokeslet) vs. $1/r$ (Stokeslet)

- **Swimming-by-jumping at the small scale produces a hydrodynamic disturbance with much smaller spatial extension and shorter temporal duration than that produced by a same-size copepod cruising steadily at the same average translating velocity. Hence, small copepods in jump-swimming are much less detectable by rheotactic predators.**

- **High Froude propulsion efficiency (0.94-0.98) obtained by CFD for individual power strokes of copepod jumps indicates the wasted mechanical energy for propulsion is tiny.**

- **Consequences of an extremely unsteady propulsion strategy at the small scale can be quite counter-intuitive.**

Summary

- An impulsive stresslet model has been developed to model the flow associated with a copepod repositioning jump. The jumping flow is characterized by two counter-rotating viscous vortex rings of similar intensity, one in the wake of the copepod and one around the body. The only model parameter, the strength of the impulsive stresslet (*M*), has been determined to be: $M = U_{max} \times V_{copepod} \times D_{jump}$, by fitting the model to the PIV flow data.

- At jump onset the flow field associated with a copepod repositioning jump declines much faster with distance to the source ($1/R^4$) than the feeding current ($1/R$) created by a negatively buoyant copepod and the swimming current ($1/R^2$) created by a neutrally buoyant copepod.

- Applying the impulsive stresslet model to an observed data set shows that a small copepod traveling by a consecutive train of small jumps creates a flow field with smaller volume of influence (i.e. the region over which flow velocity is greater than a threshold velocity) than that associated with the same copepod assumed to swim continuously at the same averaged traveling speed. The copepod adopts a jump distance according to the traveling distance of the body vortex ring within one jump interval.

Summary (continued)

- CFD simulation shows that mechanical energy cost for the repositioning jump is less than 1% of the total metabolic rate and that jumping at this small scale is an efficient propulsion mode because of its high Froude efficiency (0.94 - 0.98).

- All these results provide a reasonable explanation that jumping is a widespread behavior displayed by copepods.

- The non-dimensional jump number, $N_{\text{jump}} \equiv \frac{\tau}{L^2/(4\nu)}$, characterizes the impulsiveness of jump behavior. $N_{\text{jump}} < \sim 1$ indicates the jump being impulsive enough to create viscous vortices, whereas smaller zooplankters cannot move quietly by jump-swimming.

- The properties of the viscous vortex rings are significantly different from those of the classical inviscid vortex rings. However, unlike the inviscid rings, implications of the viscous rings to animal propulsion are much less studied. The viscous vortex ring model presented here should also be applicable to impulsively created flows by many other ecologically important marine organisms, including most zooplankton, small fish larvae, and even krill operating in the low Reynolds number regime (Re 0.1-200).