A Lagrangian model of Copepod dynamics in turbulent flows

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Outline

• Single Copepod dynamics (the essential)
• Results from a Simple Experiment
• A Lagrangian Copepod Model
• Numerical experiment with Turbulence
• Analysis and Main lessons
• Perspectives
Copepods size and shape

- Group of crustaceans
- 9000 species
- size 0.5mm to 15 mm
- aspect ratio 3-5
Copepods locomotion

Main feature: **Swimming by jumps**
Copepods locomotion

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Copepods locomotion

Main feature: **Swimming by jumps**
Copepods locomotion

Jump response to light and mechanical signals

**Acartia tonsa:**
- Stimulus (dashed line)
- Initiation of the escape response (3ms delay for mechanical)
- Acceleration during initial escape ~10 g!

**Undulina vulgaris, Lenz et al., (1999)**

*Buskey et al., (2002)*

*Buskey et al., (2003)*
Copepods react to deformation rate

*Acartia tonsa* estimated threshold $\sim 0.4 \text{ s}^{-1}$

Threshold is copepod size dependent

Sensitivity to strain rate $\sim 0.025 \text{ s}^{-1}$ Woodson et al. (2005,2007)
Copepods reaction to disturbances

Copepods comfort region

Copepods reaction to disturbances

Direction of Escape

Escapes often begin with rapid reorientation away from the source of the disturbance, with maximum turning rates of about $30^\circ \text{ms}^{-1}$

*Buskey et al., (2002)*
Simple experiment

Copepods cultures at LOG Lab in Wimereux (France)
Simple experiment

Copepods cultures at LOG Lab in Wimereux (France)

Response to light stimuli of copepod “Eurytemora affinis” in still water
Jump Data Analysis (1)

Velocity track

<table>
<thead>
<tr>
<th>Time (ms)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
</tr>
<tr>
<td>5000</td>
</tr>
<tr>
<td>10000</td>
</tr>
<tr>
<td>15000</td>
</tr>
<tr>
<td>20000</td>
</tr>
</tbody>
</table>
Jump Data Analysis (2)

Zooming in...
Jump Data Analysis (2)

Zooming in...

Velocity (m/s)

Time (ms)
Jump Data Analysis (3)

The graph shows the relationship between velocity $|V|$ (in m/s) and time (in ms). The y-axis represents the velocity with logarithmic scaling, ranging from $10^{-3}$ to $10^0$, while the x-axis represents time ranging from -20 to 120 ms. The inset graph on the right shows the PDF of jump intensity vs. jump intensity (in m/s), with the x-axis ranging from 0.04 to 0.2 ms and the y-axis ranging from $10^{-1}$ to $10^2$. The data appears to exhibit a peak around 0.1 Ms. 

The graph suggests that the velocity increases rapidly with time, reaching a peak and then decreasing. The inset PDF graph indicates a distribution of jump intensities, with a higher density around 0.1 m/s. This could imply that there is a common intensity at which jumps occur, which is important for understanding the dynamics of the system.
Jump Data Analysis (4)

\[ u_J e^{-t/\tau_J}, \quad u_J = 0.0939 \text{ m/s}, \quad \tau_J = 8.87 \text{ ms} \]

\[ u_J e^{-t/\tau_J} + \text{noise}, \quad \text{noise} = 0.005 \text{ m/s} \]
Jump Data Analysis (4)

\[ u_J e^{-t/\tau_J}, \ u_J = 0.0939 \text{ m/s}, \ \tau_J = 8.87 \text{ ms} \]

\[ u_J e^{-t/\tau_J} + \text{noise}, \ \text{noise} = 0.005 \text{ m/s} \]

\( u_J \sim 10 \text{ cm/s} \)

\( \tau_J < 10 \text{ ms} \)
Hydrodynamical forces on a particle in a flow

Point-like model

\[ \nabla \rho_p \ddot{X} = F_P + F_{AM} + F_D + F_H + F_L + F_B + F_{FX} \]

- **Pressure gradient**: \( F_P = \nabla \rho_f \frac{DU}{D\tau} \)
- **Added mass**: \( F_{AM} = \nabla \rho_f C_M \left( \frac{DU}{D\tau} - \ddot{X} \right) \)
- **Stokes drag**: \( F_D = 6 \pi a \mu (U - \dot{X}) \)
- **History drag**: \( F_H = 6 a^2 \sqrt{\pi} \nu \int_0^\tau \frac{1}{\sqrt{T - \tau}} \frac{d(U - \dot{X})}{d\tau} d\tau \)
- **Lift**: \( F_L = \nabla \rho_f C_L (U - \dot{X}) \times \Omega \)
- **Buoyancy**: \( F_B = \nabla (\rho_p - \rho_f) g \hat{e}_z \)
- **Faxen**: \( F_{Fx} : \left( \frac{DU}{D\tau}, U \right) \rightarrow \left( \langle \frac{DU}{D\tau} \rangle \nu, \langle U \rangle s \right) \)
Hydrodynamical forces on a particle in a flow (2)

Point-like model

\[ \nabla \rho_p \ddot{X} = F_p + F_{AM} + F_D + F_H + F_L + F_B + F_{FX} \]

pressure gradient  added mass  Stokes drag  History drag  Lift  Buoyancy  Faxen
Hydrodynamical forces on a particle in a flow (2)

Major approximations

\[ \nabla \rho_p \ddot{X} = F_P + F_{AM} + F_D + F_H + F_L + F_R + F_{FX} \]

- pressure gradient
- added mass
- Stokes drag
- History drag
- Lift
- Buoyancy
- Faxen
Hydrodynamical forces on a particle in a flow (2)

Major approximations

\[ \mathcal{V} \rho_p \ddot{X} = F_P + F_{AM} + F_D + F_H \]

- pressure gradient
- added mass
- Stokes drag
- History drag
- Lift
- Buoyancy
- Faxen

\[ \ddot{X} = \frac{1}{\tau_p} (U - \dot{X}) \]

\[ \tau_p = \frac{2}{9} \frac{\rho_p a^2}{\rho_f \nu} \]

[Diagram showing a particle with dimensions 2a]
Hydrodynamical forces on a particle in a flow (2)

Major approximations

\[ \mathbf{V} \rho_p \ddot{\mathbf{X}} = -\nabla p + F_{AM} + F_D + F_H + F_L + F_R + F_{FX} \]

- pressure gradient
- added mass
- Stokes drag
- History drag
- Lift
- Buoyancy
- Faxen

Formal solution

\[
\dot{\mathbf{X}}(T) = e^{-T/\tau_p} \int_0^T \frac{e^{t/\tau_p}}{\tau_p} \mathbf{U}(t) dt + \dot{\mathbf{X}}(0) e^{-T/\tau_p}
\]

\[ \tau_p = \frac{2 \rho_p a^2}{9 \rho_f \nu} \]
Hydrodynamical forces on a particle in a flow (2)

Major approximations

\[ \mathcal{V} \rho_p \ddot{X} = \mathbf{F}_P + \mathbf{F}_{AM} + \mathbf{F}_D + \mathbf{F}_H + \mathbf{F}_L + \mathbf{F}_R + \mathbf{F}_{FX} \]

- pressure gradient
- added mass
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Formal solution

\[ \dot{X}(T) = e^{-T/\tau_p} \int_0^T \frac{e^{t/\tau_p}}{\tau_p} U(t) dt + \dot{X}(0) e^{-T/\tau_p} \]

Initial condition

\[ \dot{X}(0) = U(0) + U_J \]

Slowly varying

\[ \dot{X}(T) \approx U(0) + U_J e^{-T/\tau_p} \]
Hydrodynamical forces on a particle in a flow (2)

Major approximations

\[ \mathbf{N} \rho_p \ddot{\mathbf{X}} = \mathbf{F}_P + \mathbf{F}_{\text{AM}} + \mathbf{F}_D + \mathbf{F}_H + \mathbf{F}_L + \mathbf{F}_R + \mathbf{F}_{\text{FIX}} \]

- Pressure gradient
- Added mass
- Stokes drag
- History drag
- Lift
- Buoyancy
- Faxen

\[ \ddot{\mathbf{X}} = \frac{1}{\tau_p} (\mathbf{U} - \dot{\mathbf{X}}) \]

\[ \tau_p = \frac{2 \rho_p a^2}{9 \rho_f \nu} \]

Formal solution

\[ \dot{\mathbf{X}}(\mathcal{T}) = e^{-\mathcal{T}/\tau_p} \int_0^{\mathcal{T}} \frac{e^{t/\tau_p}}{\tau_p} \mathbf{U}(t) dt + \dot{\mathbf{X}}(0) e^{-\mathcal{T}/\tau_p} \]

Initial condition

\[ \dot{\mathbf{X}}(0) = \mathbf{U}(0) + \mathbf{U}_J \]

Slowly varying

\[ \dot{\mathbf{X}}(\mathcal{T}) \simeq \mathbf{U}(0) + \mathbf{U}_J e^{-\mathcal{T}/\tau_p} \]

Our guess

\[ \tau_p \sim \tau_J \]
A minimal model

\[ \dot{x}(t) = u(x(t), t) + J(t, t_i, t_e, \dot{\gamma}, p) \]

- copepod velocity
- fluid velocity
- Jump velocity term

Modified Chlamydomonas Model
A minimal model

\[ \dot{x}(t) = u(x(t), t) + J(t, t_i, t_e, \dot{\gamma}, p) \]

**Modified Chlamydomonas Model**

\[ J(t, t_i, t_e, \dot{\gamma}, p) = H[\dot{\gamma}(t_i) - \dot{\gamma}_T] H[t_e - t] u_J e^{\frac{t_i - t}{\tau_J}} p(t_i) \]

- **copepod velocity**
- **fluid velocity**
- **Jump velocity term**
- **shear-rate trigger**
- **inhibition time**
- **exponential decay**
- **orientation**

**jump initial time**

\[ t_i = t \quad \text{if} \quad (\dot{\gamma}(t) > \dot{\gamma}_T) \cap (t > t_e) \]

**jump end time**

\[ t_e = t_i + c \tau_J = t_i + \log(10^2) \tau_J \]

**upper shear-rate threshold value**

\[ \dot{\gamma}_T \]

\[ \dot{\gamma} = \sqrt{2S : S} \]
A minimal model (orientation)

Sphere

\[ \dot{\mathbf{p}}(t) = \Omega \cdot \mathbf{p}(t) \quad \Omega_{ij} = \frac{1}{2}(\partial_i u_j - \partial_j u_i) \]
antisymmetric gradient tensor

Ellipsoid: Jeffery equation

\[ \dot{\mathbf{p}}(t) = \left( \Omega + \frac{\alpha^2 - 1}{\alpha^2 + 1} \left( \mathbf{S} - \mathbf{p}^T(t) \cdot \mathbf{S} \cdot \mathbf{p}(t) \right) \right) \cdot \mathbf{p}(t) \]

\[ S_{ij} = \frac{1}{2}(\partial_i u_j + \partial_j u_i) \quad \text{symmetric gradient tensor} \]

\[ \alpha \equiv l/d \quad \text{Aspect ratio} \]
A minimal model (summary)

Model assumptions:

- Rigid particle (spherical or ellipsoidal)
- Neutral, homogeneous density
- Hydrodynamical forces: only Stokes Drag
- Passive orientation
- Fixed response to external flow disturbances
- React to high shear-rate intensity (i.e. scalar single threshold)
- No-memory of previous jumps

Model parameters: $u_j$, $\tau_j$, $\dot{\gamma}_T$, $(t_e-t_i)$
Lagrangian Copepods (LC) in a turbulent flow

In turbulent ocean flows:

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<thead>
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Lagrangian Copepods (LC) in a turbulent flow

In turbulent ocean flows:

\[
\begin{array}{|c|c|c|c|}
\hline
\text{Parameter} & \text{Unit} & \text{Range} & \text{Reference} \\
\hline
\nu & m^2s^{-1} & \sim 10^{-6} & 10^{-6} \\
\epsilon & m^2s^{-3} & 10^{-8} \quad 10^{-4} & 10^{-6} \\
\eta & m & 3 \times 10^{-3} \quad 3 \times 10^{-4} & 10^{-3} \\
\tau_\eta & s & 10 \quad 0.1 & 1 \\
\omega_\eta & ms^{-1} & 3 \times 10^{-4} \quad 3 \times 10^{-3} & 10^{-3} \\
Re_\lambda & - & \mathcal{O}(10^2) & \\
\hline
\end{array}
\]

\[
\frac{u_J}{u_\eta} \sim O(10^2)
\]

\[
\frac{\tau_J}{\tau_\eta} \sim O(10^{-2})
\]

\[
\tau_\eta \dot{\gamma} T \sim O(1)
\]
Lagrangian Copepods (LC) in a turbulent flow

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Model Parameter Space

\[ u_J/u_\eta \sim O(10^{2}) \]
\[ \tau_J/\tau_\eta \sim O(10^{-2}) \]
\[ \tau_\eta \dot{\gamma} T \sim O(1) \]
Numerical Experiment

Lagrangian — Eulerian

LC model
\[ \dot{x}(t) = u(x(t), t) + J(t, t_i, t_e, \gamma, p) \]

Tracking of \( \sim 10^6 \) LC families with different
\[ u_j, \quad \gamma T, \quad \tau_j \sim 10^{-2} \tau_\eta \]

Homogeneous Isotropic Turbulence
\[ \partial_t u + u \cdot \nabla u = -\nabla p/\rho + \nu \Delta u + f \]
\[ \nabla \cdot u = 0 \]

pseudo-spectral algorithm
\[ \text{Re}_\lambda \sim 80 \]
\[ N = 128^3 \]
3-periodic cube
Numerical Experiment

Lagrangian — Eulerian

LC model
\[ \dot{x}(t) = u(x(t), t) + J(t, t_i, t_e, \dot{\gamma}, p) \]

Homogeneous Isotropic Turbulence
\[ \partial_t u + u \cdot \nabla u = -\nabla p/\rho + \nu \Delta u + f \]
\[ \nabla \cdot u = 0 \]

Tracking of $\sim 10^6$ LC families with different
\[ u_J \]
\[ \dot{\gamma}_T \]
\[ \tau_J \sim 10^{-2} \tau_\eta \]

Will we see clusters?

pseudo-spectral algorithm
\[ \text{Re}_\lambda \sim 80 \]
\[ N = 128^3 \]
3-periodic cube
Numerical Experiment

Lagrangian — Eulerian

LC model
\[ \dot{x}(t) = u(x(t), t) + J(t, t_i, t_e, \dot{\gamma}, p) \]

Tracking of $\sim 10^6$ LC families with different

\[ u_j \]
\[ \dot{\gamma}_T \]
\[ \tau_j \sim 10^{-2} \tau_\eta \]

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LC model
\[ \dot{x}(t) = u(x(t), t) + J(t, t_i, t_e, \dot{\gamma}, \rho) \]

Tracking of \( \sim 10^6 \) LC families with different
\[ u_J \]
\[ \dot{\gamma}_T \]
\[ \tau_J \sim 10^{-2} \tau_\eta \]

Homogeneous Isotropic Turbulence
\[
\partial_t u + u \cdot \nabla u = -\nabla p/\rho + \nu \Delta u + f
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\[ \nabla \cdot u = 0 \]

pseudo-spectral algorithm
\[ \text{Re}_\lambda \sim 80 \]
\[ N = 128^3 \]
3-periodic cube
Numerical Experiment

Lagrangian — Eulerian

LC model
\[ \dot{x}(t) = u(x(t), t) + J(t, t_i, t_e, \dot{\gamma}, \rho) \]

Tracking of \(~10^6\) LC families with different

\[ u_J \]
\[ \dot{\gamma}_T \]
\[ \tau_J \sim 10^{-2} \tau_\eta \]

Homogeneous Isotropic Turbulence
\[ \partial_t u + u \cdot \nabla u = -\nabla p/\rho + \nu \Delta u + f \]
\[ \nabla \cdot u = 0 \]

pseudo-spectral algorithm
\[ Re_\lambda \sim 80 \]
\[ N = 128^3 \]
3-periodic cube
Spatial distribution

2D slice of thickness $\eta$, Jump intensity $u_J/u_\eta = 250$, $\tau_J = 10^{-2}\tau_\eta$

Jump shear-rate threshold

1) **Low**, many jumps, few dense islands

$\tau_\eta \dot{\gamma}_T = 0.35$
2D slice of thickness $\eta$, Jump intensity $u_J/u_\eta = 250$, $\tau_J = 10^{-2}\tau_\eta$

Jump shear-rate threshold

1) **Low**, many jumps, few dense islands

2) **Intermediate**, efficient escape, sheet-like clusters

$\tau_\eta \dot{\gamma}_T = 0.92$
Jump shear-rate threshold

1) **Low**, many jumps, few dense islands

2) **Intermediate**, efficient escape, sheet-like clusters

3) **High**, efficient avoiding of extreme events, fading clusters

2D slice of thickness $\eta$, Jump intensity $u_J/u_\eta = 250$, $\tau_J = 10^{-2} \tau_\eta$
Movie

$t/\tau_\eta = 0$

$\tau_\eta \dot{\gamma}_T = 0.92$

185 $\eta$

4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
Movie

\[ t/\tau_\eta = 0 \]

\[ \tau_\eta \dot{\gamma}_T = 0.92 \]
Grassberger-Procaccia $D_2$

$$C(r) = \frac{2}{N(N-1)} \sum_{i<j} H(r - |X_i - X_j|)$$

$$D_2 = \lim_{r \to 0} \frac{\log C(r)}{\log r}$$

- **peak velocity**
- **intensity**
- **low mobility**
- **low reactivity**
- **high mobility**
- **high reactivity**
- **shear rate threshold**
Correlation Dimension

$D_2$ vs. peak velocity intensity

Saturation for huge values of peak jump intensity

$u_J > u_{\text{rms}} \sim 30 u_\eta$
Correlation Dimension

$D_2$ vs. peak velocity intensity

$D_2$ vs. shear rate threshold

Saturation for huge values of peak jump intensity
$u_j > u_{rms} \sim 30 \ u_\eta$

Optimal threshold value why?
Clustering mechanism (1)
1) Probability of a successful jump

\[ \sim \mathcal{V} \dot{\gamma} < \dot{\gamma}_T \]

volume of comfort regions

Clustering mechanism (1)
Clustering mechanism (1)

1) Probability of a successful jump

\[ \sim V \dot{\gamma} < \dot{\gamma}_T \]

volume of comfort regions

2) Rate of jumps

\[ \sim V \dot{\gamma} > \dot{\gamma}_T \]

volume of alert regions
Clustering mechanism (1)

1) Probability of a successful jump
\[ \sim \mathcal{V}_{\dot{\gamma} < \dot{\gamma}_T} \]
(volume of comfort regions)

2) Rate of jumps
\[ \sim \mathcal{V}_{\dot{\gamma} > \dot{\gamma}_T} \]
(volume of alert regions)

3) Clustering
\[ \sim \mathcal{V}_{\dot{\gamma} < \dot{\gamma}_T} \cdot \mathcal{V}_{\dot{\gamma} > \dot{\gamma}_T} \]
\[ = \mathcal{V}_{\dot{\gamma} > \dot{\gamma}_T} \cdot (\mathcal{V}_{tot} - \mathcal{V}_{\dot{\gamma} > \dot{\gamma}_T}) \]
1) Probability of a successful jump

\[ \sim V \gamma < \gamma_T \]

volume of comfort regions

2) Rate of jumps

\[ \sim V \gamma > \gamma_T \]

volume of alert regions

3) Clustering

\[ \sim V \gamma < \gamma_T \cdot V \gamma > \gamma_T \]

\[ = V \gamma > \gamma_T \cdot (V_{tot} - V \gamma > \gamma_T) \]

Maximum for

\[ V \gamma > \gamma_T = V_{tot} / 2 \]
Clustering mechanism (2)

Fraction of time Time spent in alert regions \( \dot{\gamma} > \dot{\gamma}_T \)

\[
\frac{\langle T_{\gamma} \rangle_{\eta T}}{T_{tot}} = \frac{\nu_{\gamma > \gamma_T}}{\nu_{tot}} / 2
\]
PDF of Velocity

Tracers

$\tau_\eta \dot{\gamma}_T = 0.21$

0.5

0.7

1.2

1.77

PDF($|\dot{x}_i/u_\eta|$)
PDF of Velocity

\[ \text{PDF}(|\dot{x}_i/u_\eta|) \]

\[ \ddot{x} = U + \alpha \; p \; u_J e^{-t/\tau_J} \]

- Gaussian random variable
- Jumping fraction
- Random vector
- Flat random [0, t_e]
PDF of Velocity

\[ \dot{x} = U + \alpha \mathbf{p} u J e^{-t/\tau_J} \]

- \( \dot{x} \): Gaussian random variable
- \( \alpha \mathbf{p} u J e^{-t/\tau_J} \): random vector
- \( \tau_T \): flat random variable [0, \( t_e \)]

Tracers
- \( \tau_{\eta} \dot{\gamma}_T = 0.21 \)
- \( 0.5 \)
- \( 0.7 \)
- \( 1.2 \)
- \( 1.77 \)
PDF of Velocity

\[ \dot{x} = U + \alpha p u J e^{-t/\tau_J} \]

Gaussian random variable
jumping fraction?
random vector
flat random \([0, t_e]\)

Tracers
\( \tau_\eta \dot{\gamma}_T = 0.21 \)
0.5
0.7
1.2
1.77

Deduced \(\alpha\) fraction of jumping particles
Summary

- LC model exhibits clustering in turbulence $D_2 \sim 2.3$
- Necessary conditions for Clustering:
  1) high jump speed $u_J > u_{rms}$
  2) sharp sensitivity to shear rate $O(\tau_\eta^{-1})$

- Clustering comes from inhomogeneity rather than anisotropy of the model (Excluded volume mechanism)
- Different mechanism from the one identified for motile algae (gyrotaxis induced).

LC Model v1.0
Many possible extensions...
Effect of Aspect ratio

Particle orientation dynamics
no impact on clustering
or velocity distribution
What if one varies $t_e - t_i = \tau_{\text{wait}}$?
Effect of jump time latency

What if one varies $t_e - t_i = \tau_{\text{wait}}$?
Effect of jump time latency

What if one varies $t_e - t_i = \tau_{\text{wait}}$?
Effect of jump time latency

What if one varies $t_e - t_i = \tau_{\text{wait}}$?

Which effect on clustering?
Effect of jump time latency (2)

Only a prompt reaction leads to clusters
Correlation: time gap with peak velocity gap

\[ \Delta u = |u_{\text{peak}}(n+1) - u_{\text{peak}}(n)| \]

\[ \Delta t = t_{\text{jump}}(n+1) - t_{\text{jump}}(n) \]
Jump intensity vs latency in experimental data

Correlation: time gap with peak velocity gap

\[ \Delta t = t_{\text{jump}}(n+1) - t_{\text{jump}}(n) \]

\[ \Delta u = |u_{\text{peak}}(n+1) - u_{\text{peak}}(n)| \]
Necessary conditions for Clustering:

1) high jump speed $u_j > u_{rms}$
2) sharp sensitivity to shear rate $O(\tau_\eta^{-1})$
3) high jump frequency $<< \tau_\eta$

- If reaction is quick, particle orientation is not a crucial aspect
- Eulerian modelling should be possible in these conditions

*Effective Diffusivity (local share-rate)*

**arXiv:1601.01438**

A Lagrangian model of Copepod dynamics: clustering by escape jumps in turbulence

Hamidreza Ardestiri, Ibtissem Benkeddat, François G. Schmitt, Sami Souissi, Federico Toschi, Enrico Calzavarini
Conclusions & Perspectives

- Necessary conditions for Clustering:
  1) high jump speed $u_J > u_{\text{rms}}$
  2) sharp sensitivity to shear rate $O(\tau_\eta^{-1})$
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- If reaction is quick, particle orientation is not a crucial aspect
- Eulerian modelling should be possible in these conditions

*Effective Diffusivity*(local share-rate)

Model refinements
- Memory effect (explore delay - amplitude relation)
- Considering finite-size of domain of perception

Test the model against real measurements in turbulence
(Needs new experimental data)
Thank you!

\[ t/\tau_\eta = 0 \]

\[ \tau_\eta \dot{\gamma}_T = 0.92 \]
Thank you!

\[ t/\tau_\eta = 0 \]

\[ \tau_\eta \dot{\gamma}_T = 0.92 \]
Back to data analysis

jump time-gap statistics

\[ \Delta t = t_{\text{jump}}(n+1) - t_{\text{jump}}(n) \]
jump time-gap statistics

\[ \Delta t = t_{\text{jump}}(n+1) - t_{\text{jump}}(n) \]