

# Mechanical modelling of marine planktonic copepod dynamics in fluid flows

H. Ardeshiri<sup>a,b</sup>, F. G. Schmitt<sup>b</sup>, S. Souissi<sup>b</sup>, F. Toschi<sup>c,d</sup>, E. Calzavarini<sup>a</sup>

a. Univ. Lille, CNRS, FRE 3723, LML, Laboratoire de Mécanique de Lille, F 59000 Lille, France

b. Univ. Lille, CNRS, Univ. Littoral Cote d'Opale, UMR 8187, LOG, Laboratoire d'Océanologie et de Géoscience, F 62930 Wimereux, France

c. Department of Applied Physics and Department of Mathematics and Computer Science, Eindhoven University of Technology, 5600 MB, Eindhoven, The Netherlands

d. Istituto per le Applicazioni del Calcolo CNR, Via dei Taurini 19, 00185 Rome, Italy

## Résumé :

*Les copépodes planctoniques sont de petits crustacés qui présentent une motilité caractérisée par des phases quiescentes alternées par des régimes de déplacements rapides, dits sauts, produits par des puissants mouvements de natation. Le comportement de saut a été associé à une réaction de fuite à des perturbations d'écoulement dues à de grands prédateurs (tels que des larves de poissons) ou à d'autres dangers externes (par exemple une forte turbulence). A travers des travaux à la fois expérimentaux et numériques, nous étudions comment un comportement de saut crée de la concentration préférentiel de copépodes dans un environnement turbulent. Nous passons en revue les résultats les plus récents obtenus par l'analyse d'un modèle numérique fondé sur l'approche lagrangienne. En outre, nous proposons une extension d'un tel modèle discret au niveau de la population au moyen d'une description eulérienne continue.*

## Abstract :

*Planktonic copepods are small crustaceans that display a motility characterised by quiescent phases alternated by regimes of fast displacements, dubbed jumps, produced by powerful swimming strokes. The jump behaviour has been associated to a reaction of escape from flow disturbances due to large predators (such as fish larvae) or other external dangers (e.g. strong turbulence). Through a combined experimental and numerical study, we investigate how the jumping behaviour creates small-scale patchiness of copepods in a turbulent environment. We review the most recent results obtained by the analysis an individual based numerical model built on the Lagrangian approach. Further, we propose an extension of such a discrete model to the population level by means of a continuous Eulerian description.*

**Mots clefs : Hydrodynamic turbulence, Particle laden flows, Swimmers, Plankton, Marine Ecology**

# 1 Introduction

Copepods are often described as the largest and most variegated group of crustaceans in the aquatic environment [1]. They populate the oceans and river estuaries with a number density that can be as high as thousands individuals per litre of water. Their typical body size ranges from half to few millimetres, a length which is of the order of the dissipative scale of turbulence in the ocean ( $\eta$ ) [2, 3]. Their body mass density is very close to the one of the fluid ( $1 \text{ mg/mm}^3$ ) meaning that they are essentially neutrally buoyant [4]. Copepods possess an elongated body with few pairs of swimming legs, a tale and two receptive antennas which allow them to feel the surrounding fluid flow via mechanoreceptive hairs, called setae. Copepods can swim, their locomotion behaviour in water is characterized by the alternation of passive phases, where they are simply carried by the flow, and active phases where rapid strong displacements (called jumps) are performed. Such jumps are often the result of an escape reaction from flow perturbations. These perturbations can be produced by predators of larger size or by the fluctuations which are omnipresent in the oceanic turbulent fluid flow. Despite the fact that copepods escape response can be elicited by different types of stimuli, *e.g.*, hydrodynamical, photic and chemical ones, they appears to react almost always in the same manner : by performing a series of jumps. During the jumps copepod velocity reaches very high values, leading to a large body-scale Reynolds number ( $Re \sim 10^{2-3}$ ), which is much higher compared to the Reynolds number they have in their quiescent state (also called foraging state) ( $Re \sim 10^{0-1}$ )[5].

In 1999, Kiørboe et al. [6] and Kiørboe and Visser [7] performed series of experiments investigating the effect of swimming motion on copepods in relation to mechanical stimuli imparted by the surrounding flow. The outcome of their research was that copepods react to the shear deformation rate of the flow. The threshold value of the deformation rate for copepod species *Acartia tonsa* with 1 mm in length was reported to be  $0.4 \text{ s}^{-1}$ . However, sensitivity to strain rate (velocity gradient) was reported to be  $0.025 \text{ s}^{-1}$  by Woodson et al. [8, 9] by putting copepods species (*Acartia tonsa* and *Temora longicornis*) in a plane jet flume apparatus which mimics ocean characteristics. Notice that the threshold value appears to be copepod size dependent and is inversely proportional to copepod's size [6, 7]. Even the fact that copepods react to deformation rate is presently under discussion, recently Webster et al. [10] examined the behavioural response of *Acartia tonsa* and *Temora longicornis* in turbulent vortex, and highlighted a sensitivity to vorticity cues rather than shear deformation. Taking into account the intensity of the deformation rate as a threshold reaction criterion, Kiørboe in his book [11] made a compilation of experimental results on a plot showing the behaviour of the threshold deformation rate as a function of size. He identified two thresholds, the lower one corresponding to the regions in the flow where the ambient level of turbulence is too small (where the flow does not fluctuate) and the high threshold is associated to the predators or the fluctuations generated by turbulence. The present study will focus particularly on the latter (high threshold value), and region of the flow characterised by high deformation rates will be called alert regions. We conclude by mentioning that wide uncertainties still persist on the understanding of the spatial direction taken by a copepod through a jump. Some authors [12, 13] have reported that for a horizontally located stimuli, copepods tend to jump upward in a vertical plane, furthermore it is evident from the experimental observations that copepods rarely jump backward. For a more complete review about copepods (anatomy, locomotion, their interaction with the fluid) we refer to [14].

The goal of the present study is to propose a model system for copepods dynamics in turbulent flow and to study its salient features. The model is based on experimental measurements available in the literature [5, 15, 16, 17, 18, 19, 20] and on the ones which were performed in Laboratory of Oceanology

and Geoscience (LOG) in France. The aim is to propose a model which mimics copepods locomotion and characterizes the resulting dynamics in a flow. In section 2.1 the experimental setup is briefly explained. Then a model of copepod dynamics based on a Lagrangian approach (Lagrangian Copepod model, LC) is introduced and its implementation on turbulent flows is briefly described in sections 2.2 and 2.3. The results of the LC model are summarized in section 3.1. Later on we discuss the possibility to extend the individual based LC model to a population based model capable to describe the evolution of the concentration of the copepods in a flow, section 3.2. This proceeding ends with conclusion and perspectives.

## 2 Methods

### 2.1 Experiments

We studied copepod individuals from species *Eurytemora affinis* and *Acartia tonsa* coming from continuous cultures of these species maintained at LOG Laboratory in the period between May and June 2015. The aim of the experiments consisted in recording highly resolved copepods trajectories during jump events in still water. Experimental setup consists of a small aquarium,  $63 \times 53 \times 6 \text{ mm}^3$  in length, height and depth respectively, more bi-dimensional as possible ( $6 \text{ mm}$  in depth). The aquarium was equipped by two lateral light sources. Copepods were introduced once at a time and the light sources are manually switched on and off in order to stimulate copepods. Due to the escape reaction to the light, copepods jump and their trajectories are recorded for variable durations of few seconds up to  $23 \text{ sec}$ . The recording of the copepod displacement in the  $x - y$  vertical plane was performed by high speed camera ( $1000 \text{ frames/second}$ ). Notice that the frequency at which the lights was switched on and off, was much lower than the jump frequency of copepods and it seemed not to affect the jump behaviour but only their directions (since copepods are attracted by the visible light). Figure 1 illustrates the configuration of the experimental devices together with a test snapshot from the camera. More information on the experimental setup can be found in [14, 21]. A typical copepod velocity amplitude signal as a function

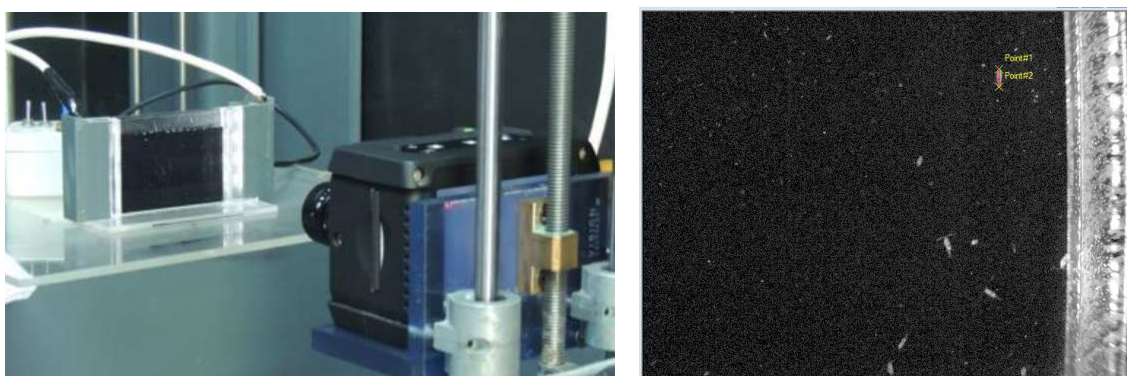


FIGURE 1 – (left) The experimental setup is composed of a rectangular aquarium filled with water, two light sources (white areas next to the dark aquarium) and a high-speed ( $1k\text{Hz}$ ) camera. The copepods trajectories in the vertical plane are extracted by means of a particle tracking velocimetry software (TEMA Motion by Image Systems). (right) A typical frame from the experiment, the labels “Point #1,2” denote the body of a copepod of estimated size  $1.05 \pm 0.05 \text{ mm}$ .

of time, and of total duration of  $15 \text{ sec}$ , can be found in Fig. 2. A zoomed-in version on the interval of  $[1 - 5] \text{ sec}$  shows how the copepod escape reaction are initiated by a sharp spike and are followed

by a decaying function (see the panel B of Fig. 2). The analysis of the probability density function of copepods velocity intensity ( $|V|$ ) suggests that the spread in such a quantity is limited. This allows to make a graph in which all the jumps are time-shifted in such a way that their peaks overlap (Fig. 3). This manner of looking at the data suggests the existence of a characteristic pattern in the evolution of the velocity intensity during the jumps.

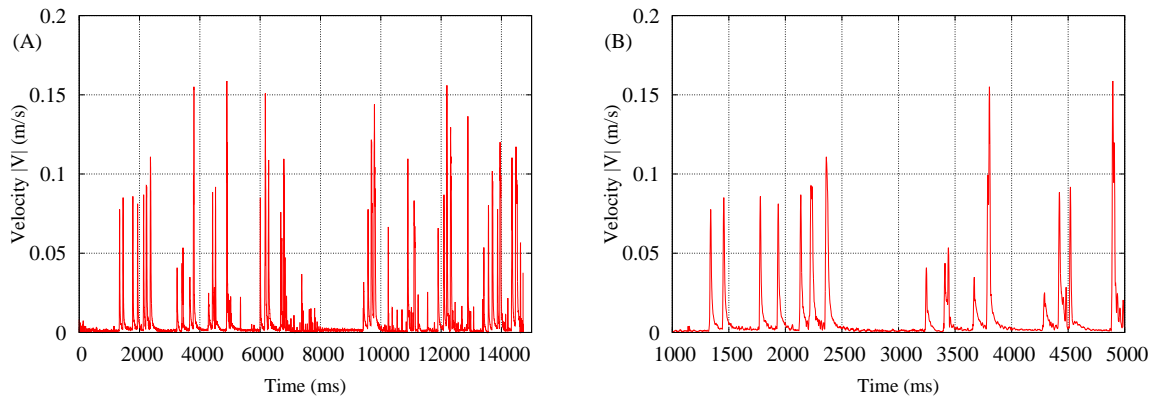


FIGURE 2 – A) Copepod velocity intensity,  $|V| = \sqrt{v_x^2 + v_y^2}$ , as a function of time for  $\sim 15$  s. B) The same quantity now zoomed-in on time  $[1, 5]$ sec.

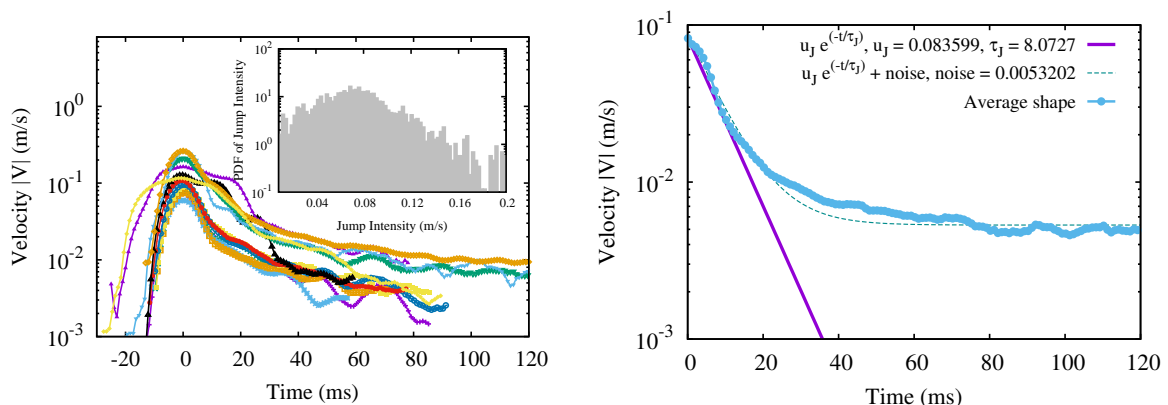


FIGURE 3 – (left) Superposition of several jumps by a shift. Almost all of the jumps decay exponentially. (Inset) The probability density function (PDF) of the jump intensity. (right) Global average shape of copepod velocity intensity. Solid line : Fitted exponential function  $u_J e^{-t/\tau_J}$  where  $u_J$  is the jump intensity and  $\tau_J$  is the decaying time of the jump. Dashed line : Same fit with the addition of a noise velocity offset.

An average performed over all the jump velocity tracks fits well with an exponential function : this is illustrated for *E. affinis* in Fig. 3. One can then estimate the average copepod jump amplitude (a very high intensity,  $u_J$  83 mm/s) and the jump decay time (very quick decay,  $\tau_J \simeq 8$  ms). We observe also the presence of a drifting noise with a negligible amplitude (about 5 mm/s) as compared to the jump intensity of copepods. Due to its small intensity, we were unable to identify if the drift was due to foraging motion of copepods or to other experimentally induced fluctuations.

The exponential decay of velocity can be linked to the hydrodynamic forces acting on copepods during the jumps. In its most coarse description, the dynamics of copepods can be thought as the balance between the acceleration imposed by a nearly instantaneous force, leading to the jump, and the fluid

drag force acting on the body. Taking as a model the equation of a small material particle in fluid flows [23] and retaining only the drag force, one can write down the following equation :

$$\ddot{\mathbf{x}}(t) = \frac{1}{\tau_p} (\mathbf{u}(t, \mathbf{x}(t)) - \dot{\mathbf{x}}(t)) \quad (1)$$

in the absence of an external fluid flow ( $\mathbf{u} = 0$ ) and with an initial condition  $\dot{\mathbf{x}}(0) = \mathbf{u}_J$  (produced by the instantaneous jump force), the resulting velocity can be written as :

$$\dot{\mathbf{x}}(\tau) \cong \mathbf{u}_J e^{-\tau/\tau_p} \quad (2)$$

where  $\tau_p$  is particle response time associated to the drag force. In case of a Stokes flow regime, it reads  $\tau_p = \frac{a^2}{3\beta\nu}$  where  $a$  is copepod effective radius,  $\nu$  is the kinematic viscosity and  $\beta = \frac{3\rho_f}{2\rho_p + \rho_f}$  represents the density ratio, here  $\simeq 1$ . An evaluation of the maximal Reynolds number reached during a jump based on the copepod size, *i.e.*,  $Re = u_J 2a/\nu$  leads here to  $Re \simeq 87$  which is well beyond the Stokes regime. Based on this observation, we are lead to associate the time  $\tau_J$ , the copepods' jump decay time that we extracted from the experiments, to an effective drag-related response time of the copepods.

## 2.2 Lagrangian copepod (LC) model system

The above presented experimental jump data analysis and available observations in the literature [5, 15, 16, 17, 18, 19, 20], can be exploited to introduce a simple model system of copepod's swimming behaviour. We use here a Lagrangian modelling approach, similar to the one adopted for the modelling of a material particle laden in a flow. In this Lagrangian model, copepods are considered to be as rigid, homogenous and neutrally buoyant particles which respond always in the same way to external flow disturbances. Copepods in this model are advected by the flow like a perfect fluid tracer, except for the time when a jump event takes place. It is further assumed that a mechanical signal with a single threshold is the only stimuli that triggers the jumps. Any other activity induced by light, food, or chemistry (*e.g.*, pheromones) are ignored here. Copepod-copepod interactions and also their mechanical feedback on the surrounding flow are neglected. Drag is the only hydrodynamical force that is taken into account. The Lagrangian copepod equation of motion, thus reads as follows :

$$\dot{\mathbf{x}}(t) = \mathbf{u}(\mathbf{x}(t), t) + \mathbf{J}(t, t_i, t_e, \dot{\gamma}, \mathbf{p}) \quad (3)$$

where  $\mathbf{u}(\mathbf{x}(t), t)$  is the velocity of the carrying fluid at time  $t$  and position  $\mathbf{x}(t)$  and where  $\mathbf{J}$  is an added velocity term that describes the active behaviour (jump) of the copepod and has to be modelled. If it is true that copepod's jump velocity decays exponentially, we still need to define a jump spatial orientation and one also has to define when the jump is triggered and when it ends. Here we introduce a set of basic rules based on few schematic ideas such that (i) a copepod jumps when it is in alert region (region where its shear rate is above a threshold,  $\dot{\gamma} > \dot{\gamma}_T$ ), (ii) it can not jump when it is already jumping and (iii) the end of jump is after a prescribed time interval which we define to be when the jump velocity has decreased one percent of the initial amplitude. These rules can be mathematically expressed as :

$$\mathbf{J}(t, t_i, t_e, \dot{\gamma}, \mathbf{p}) = H[\dot{\gamma}(t_i) - \dot{\gamma}_T] H[t_e - t] u_J e^{\frac{t_i - t}{\tau_J}} \mathbf{p}(t_i) \quad (4)$$

where  $H[x]$  denotes the Heaviside step function,  $\dot{\gamma}_T$  is a threshold value of the shear rate,  $u_J$  and  $\tau_J$  are the two characteristic parameters characterising the jump shape, its velocity amplitude ( $u_J$ ) and duration

( $\tau_J$ ) respectively and  $\mathbf{p}$  represents the orientation vector. The initial and final time of a jump are defined as :

$$t_i = t \quad \text{if} \quad (\dot{\gamma}(t) > \dot{\gamma}_T) \cap (t > t_e) \quad (5)$$

$$t_e = t_i + c\tau_J = t_i + \log(10^2)\tau_J \quad (6)$$

and the duration of a jump is  $\tau_w = t_e - t_i$  and the strain rate is then defined as  $\dot{\gamma} = \sqrt{2\mathcal{S} : \mathcal{S}}$  where  $\mathcal{S}$  is the fluid deformation rate symmetric tensor as  $S_{ij} = 1/2(\partial_i u_j + \partial_j u_i)$ . The orientation of the jump is determined by instantaneous copepod orientation at time  $t_i$ , in other words it is  $\mathbf{p}(t = t_i)$  with the copepod's orientation dynamic given by the following general equation :

$$\dot{\mathbf{p}}(t) = \boldsymbol{\Omega} \cdot \mathbf{p}(t). \quad (7)$$

Here  $\boldsymbol{\Omega}$  is the fluid rotation rate antisymmetric tensor, defined as  $\Omega_{ij} = 1/2(\partial_i u_j - \partial_j u_i)$ . We observe that this is a rather crude version of the equation for the rotation of a material particle. It assumes that the particle is spherical, that the inertia of the copepods does not play any role, and finally that copepods can not reorient themselves. Given the fact that copepods are non-spherical,  $\alpha \equiv l/d$  is the aspect ratio of copepods given by the ratio of length ( $l$ ) to diameter ( $d$ ), which is typically around 3 for *Eurytemora affinis*, a more appropriate description can resort from Jeffery's equation [24].

### 2.3 Coupling of LC model to a turbulent flow

We now want to address the question of the dynamics of copepods which are carried on by a flow and more specifically their natural environment flow. The habitat of copepods is the fluid flow in the ocean (or in river estuaries) which is most of the time in developed turbulent condition [3, 2]. For this reason, in our study we generate a turbulent flow by means of a direct numerical simulation of the incompressible Navier-Stokes equations based on a pseudo-spectral method. The simulated equations are,

$$\partial_t \mathbf{u} + \mathbf{u} \cdot \nabla \mathbf{u} = -\nabla p / \rho_f + \nu \Delta \mathbf{u} + \mathbf{f}, \quad \nabla \cdot \mathbf{u} = 0, \quad (8)$$

where  $\mathbf{u}(t, \mathbf{x}(t))$  is the fluid velocity field,  $p$  is the pressure,  $\nu$  is the kinematic viscosity,  $\rho_f$  is the fluid density and  $\mathbf{f}$  is a large scales forcing which allows to produce a statistically homogenous and isotropic turbulent flow. The computational domain we use is a box of  $128^3$  grid points which enables to reach a turbulent intensity characterised by a Taylor-Reynolds number of  $Re_\lambda \approx 80$ . We refer to Table 1 for a comparison between the typical ocean properties and the numerical values set in our simulation.

For the coupling of the Lagrangian copepod model to the Eulerian simulation of fluid-dynamics turbulence we proceed as follows. First, we choose the dissipative scales of turbulence ( $\eta$ ,  $u_\eta$ ,  $\tau_\eta$ ) as the relevant scales for the problems at hand, and we perform a similarity analysis that allows to recast the LC model in terms of three dimensionless control parameters :  $\tau_J/\tau_\eta$ ,  $u_J/u_\eta$  and  $\tau_\eta \dot{\gamma}_T$ . Second, such parameters are chosen in the physically relevant ranges :  $u_J/u_\eta \in [1, 400]$  and  $\tau_\eta \dot{\gamma}_T \in [0, 4]$ , whilst  $\tau_J/\tau_\eta = 10^{-2}$ . Third, these parameters are assigned to independent groups (called families) of LC individuals with about  $2.56 \times 10^5$  particles per family. The simulations, Eulerian and Lagrangian one, are performed simultaneously and with all the families at the same time. Note that this is possible because LC particles do not interact with each other but are only one-way coupled to the fluid flow (see [21] for extended details on the numerical implementations). More details on the implementation of the LC model in turbulent flows can be found in [14, 21].

Parameter	Unit	Range		Our simulations
$\nu$	$m^2 s^{-1}$	$\sim 10^{-6}$		$10^{-6}$
$\epsilon$	$m^2 s^{-3}$	$10^{-8}$	$10^{-4}$	$10^{-6}$
$\eta$	$m$	$3 \times 10^{-3}$	$3 \times 10^{-4}$	$10^{-3}$
$\tau_\eta$	$s$	10	0.1	1
$u_\eta$	$ms^{-1}$	$3 \times 10^{-4}$	$3 \times 10^{-3}$	$10^{-3}$
$Re_\lambda$	–	$\mathcal{O}(10^2)$		80

TABLE 1 – Reference properties of the ocean turbulent flow as from [3, 2].  $\epsilon$  is the mean turbulent energy dissipation rate,  $\eta$ ,  $\tau_\eta$  and  $u_\eta$  are the turbulence space, time and velocity dissipative scales.  $Re_\lambda$  is the Taylor-scale based Reynolds number. Their approximate range of variability is given together with the reference values chosen for the similarity analysis in the present study.

### 3 Results

#### 3.1 The LC model phenomenology

The aim of this section is to offer a concise overview of the results obtained so far by the study of the LC model. We refer to [14] for a more complete description. First, the LC single-point velocity statistics (probability density function of copepods velocity) displays a qualitative agreement with available experimental observations of copepods in turbulence. Their statistics does not follow a Gaussian distribution exhibited by fluid tracers and such a deviation depends both on the jump intensity and on jump duration. Conversely, increasing the level of turbulence reduces the non-Gaussian effects. Similar trends have been measured in recent experiments at ETH, Zurich by Michalec et al. [25]. Second, the LC model in turbulence leads to preferential concentration of copepods due to the escape reaction from regions with high strain rate intensities. This is the most remarkable feature of the LC model since the clustering mechanism displayed is due to the non-homogeneity in space while the model is isotropic, which is in stark contrast with the clustering mechanism observed for motile algae given by the gyrotactic effect, which is a non-isotropic effect of the gravity [26]. We further quantified the clustering of LC, via the fractal dimension  $D_2$ . We showed that  $D_2$  can be as low as  $\sim 2.3$  and that it critically depends on the shear-rate sensitivity of the proposed LC model, in particular it exhibits a minimum in a narrow range of shear-rate values [21]. The preferential concentration of these microorganisms is ecologically crucial since this can directly affect many biological process which are typically determined by the individual interaction or inter-species contact rate. For instance the formation of patches by an escape reaction, can increase the reproduction of copepods due to the increase in contact rate with mates. However this might have a negative effect and can increase the competition between microorganisms for food uptake.

Third, the encounter rate of copepods in a developed turbulent flow with intensity comparable to the one found in copepods' habitat is numerically investigated [22]. Our analysis shows that the encounter rate for copepods of typical perception radius of  $\sim \eta$ , where  $\eta$  is the dissipative scale of turbulence, can be increased by a factor up to  $\sim 10^2$  compared to the one experienced by passively transported fluid tracers. Furthermore, we address the effect of introducing in the LC model a minimal waiting time between consecutive jumps. It is shown that any encounter-rate enhancement is lost if such a time goes beyond the dissipative time-scale of turbulence,  $\tau_\eta$ . Because typically in the ocean  $\eta \sim 10^{-3} m$  and  $\tau_\eta \sim 1 s$ , this provides stringent constraints on the turbulent-driven enhancement of encounter-rate due to a purely mechanical induced escape reaction. A final notable result is that the particles orientational dynamics has no effect on the PDF of velocity and on the correlation dimension of copepods. This negligible im-

pact of orientation for the case examined here, suggests the possibility to formulate an accurate Eulerian mean-field particle model based on the introduction of a space-dependent effective diffusivity. We now focus on this in the following.

### 3.2 Towards a copepod population model system

The individual based description of copepods offered by the Lagrangian model, is suitable when addressing questions about the single organism displacement in turbulence or questions about encounter rates or accumulation of organisms. Such a description becomes non-viable in computational terms if the focus is on the behaviour of a large population which can occupy spatial domains larger than the integral scale of the turbulent flow (roughly speaking above the meter scale). In the latter situation it would be desirable to adopt a mean-field approach and to be able to describe the evolution of a continuous positive definite field accounting for the local population concentration. Such an approach, called in short Eulerian, is more common in the oceanographic studies, where the involved scales go much beyond the meter size and involve populations of millions of organisms. A notable example is the description of the evolution of thin plankton layers formed in the upper-ocean, which extends till  $O(10^{1-2})m$  below the sea level. While rudimentary Eulerian model for the less mobile phytoplankton are already available, the modelling of the zooplankton, due to its inherent high-motility, represents a more challenging task. The goal of this section is to propose an Eulerian model system for the evolution of the concentration of copepods that properly upscale the Lagrangian copepod (LC) model previously discussed.

In [21] we have observed that the shape of the particle, hence the orientation of jumps seems not to play a major role in the resulting particle dynamics. In fact it only marginally affects the small scale clustering as quantified by the correlation dimension  $D_2$ . This justifies a modelling approach in which copepods motility is parametrised in term of a diffusion coefficient. The starting equation to be considered for the description of copepods concentration  $C$  is the advection-diffusion equation :

$$\partial_t C + \mathbf{u} \cdot \nabla C = \mathcal{K} \Delta C \quad (9)$$

where  $C(t, \mathbf{x}(t))$  represents the fraction of individuals per unit volume,  $\mathbf{u}$  is the advecting incompressible fluid velocity field and  $\mathcal{K}$  is a suitable effective diffusion coefficient. However, the diffusion term needs to be examined in detail since it has to correctly model the copepod jump dynamics. Because jumps are performed only in alert regions, it is clear that the diffusion coefficient has to carry a spatial dependence, not directly but through its dependancy on the strain rate ( $\dot{\gamma}$ ). A space dependence diffusivity calls for a modification of the advection diffusion equation presented above, because it can be easily shown that starting from a homogeneous population  $C = const.$ , eq. (9) would not produce any localisation of copepods, even if  $\mathcal{K}$  was a time and space dependent function. Two alternatives modifications of (9) are available and can be considered, the first is to write the diffusion term as  $\nabla \cdot (\mathcal{K} \nabla C)$ , a second way is to express this term as  $\Delta(\mathcal{K}C)$  [27, 28]. These two plausible ways of expressing the spatial-dependent diffusion term model different individual behaviours. Which one should be used ? The choice shall be based on the physical interpretation. Our aim here is to find an equivalent Eulerian representation for the Lagrangian copepod model : the key feature of this model is that an initial homogenous distribution of copepods evolves into a non-homogenous spatial distribution (clustering). In other words the global variance of  $C$  can increase as a function of time. This request can be satisfied only by the



diffusive term  $\Delta(\mathcal{K}C)$ . In fact when expanded it gives :

$$\Delta(\mathcal{K}C) = C\Delta\mathcal{K} + \nabla\mathcal{K}\nabla C + \nabla(\mathcal{K} \cdot \nabla C). \quad (10)$$

While the terms involving spatial derivatives of the concentration ( $\nabla C$  and  $\Delta C$ ) are zero in a homogeneous population, the extra term  $C\Delta\mathcal{K}$  is responsible for the growth of  $C$  in regions around local maxima of the diffusivity ( $\Delta\mathcal{K} > 0$ ). We therefore adopt the dynamical equation :

$$\partial_t C + \mathbf{u} \cdot \nabla C = \Delta(\mathcal{K}C) \quad (11)$$

Note that in the context of zooplankton studies a similar continuous model system has been proposed in [29] by upscaling a much alike random jump motility individual model in a quiescent (no-flow) environment.

We already mentioned that the diffusivity  $\mathcal{K}$  depends on space not directly but through its dependence on the strain-rate  $\dot{\gamma}$ . The next step in modelling is therefore to introduce a functional form for such a dependence. In view of numerical implementation of the model it is desirable to have a smooth rather than a discontinuous  $\mathcal{K}(\dot{\gamma})$  dependency. As a first attempt we choose an hyperbolic step function of the following form :

$$\mathcal{K}(\dot{\gamma}) = K_s + \frac{K_a - K_s}{2} \left( 1 + \tanh \left( \frac{\dot{\gamma} - \dot{\gamma}_T}{\delta\dot{\gamma}} \right) \right) \quad (12)$$

Here the parameter  $K_a$  indicates the effective diffusivity in alert regions while  $K_s$  is an additional (optional) small diffusivity in the safe regions ( $K_s \ll K_a$ ). The alert region are defined by  $\dot{\gamma} > \dot{\gamma}_T$ , while the parameter  $\delta\dot{\gamma}$  corresponds to the width of the transition in terms of the strain-rate. Indeed, even if the boundary between alert and safe regions is sharp, given by the contour lines where  $\dot{\gamma}(\mathbf{x}) > \dot{\gamma}_T$ , the transition between a high and low diffusivity region is always smoother because jumping copepods can enter into safe regions with a high velocity and vice versa (when  $K_s > 0$ ) some organisms in safe regions can diffuse in the alert ones.

In order to obtain the numerical value of the parameter  $K_a$ , the standard link between the Mean Squared Displacement (MSD) of a Brownian particle and diffusivity can be exploited. Here we consider LC particles that are permanently set in alert state and in an environment without flow. We then evaluate

$$K_a = \frac{\langle (\mathbf{x}(t) - \mathbf{x}(t_0))^2 \rangle}{2D(t - t_0)}, \quad (13)$$

where  $\mathbf{x}(t_0)$  refers to the initial copepod position at the initial time  $t_0$ ,  $D$  is the dimension of the domain (here  $D = 2$ ), and the symbol  $\langle . . . \rangle$  refers to ensemble average over LC independent particles. We observe that the link expressed by eq. (13) can hold only approximately, since it ignores the fact that the jump velocity intensity has a time dependence.

We now test the proposed Eulerian population model in a simple setup. We consider the Taylor-Green vortex flow (TGV) (also known as cellular flow or Solomon and Gollub flow [30]) which is a laminar, steady, incompressible, 2-dimensional flow with periodic boundary conditions. The cellular flow is composed of a periodic array of eddies in square cells of size  $L$  and it can be specified by the following

velocity field,

$$\begin{cases} u_x = U_0 \sin\left(\frac{\pi x}{L}\right) \cos\left(\frac{\pi y}{L}\right) \\ u_y = -U_0 \cos\left(\frac{\pi x}{L}\right) \sin\left(\frac{\pi y}{L}\right). \end{cases} \quad (14)$$

In such a flow we define alert and safe areas based on the threshold value  $\dot{\gamma}_T = \frac{1}{3}\dot{\gamma}_{max}$ , where  $\dot{\gamma}_{max}$  denotes the maximum strain-rate in the flow. Since the velocity field is time independent such regions are here fixed once for all. The parameter  $\delta\dot{\gamma}$  is arbitrary set to a value  $\ll \dot{\gamma}_{max}$ , here  $\delta\dot{\gamma} = \frac{1}{20}\dot{\gamma}_{max}$ . The diffusion coefficient of copepods in alert regions  $K_a$  is estimated by means of eq. (13) on a LC setting characterised by the parameters  $u_J = 250 U_0$  and  $\tau_J = 10^{-2} L/U_0$ . This leads to the value  $K_a = 130 U_0 L$ . We also add a small random displacement in the LC model, such that in the safe region this leads to a diffusivity  $K_s = 0.01 U_0 L$ . This simplifies the numerical implementation of the Eulerian simulation. The advection-diffusion equation (11) is solved via a standard pseudo-spectral method. The field  $C$  is initialised to be constant in space ( $C_h$ ) and the velocity field  $\mathbf{u}$  is given by the TGV above described flow.

Figure 4 shows a comparison between the stationary state of the population concentration as derived from the LC model (panel B) and from the Eulerian one with the above described parameters (panel A). It is evident that, despite the fact that a non uniform distribution develops, the Eulerian model can not reproduce the same features of the Lagrangian model. We thought that this may come from the delicate tuning of the parameters in the model, such as  $\delta\dot{\gamma}$  and  $K_a$ . A second simulation with the value of diffusivity  $K_a = 1 U_0 L$  (panel C) offers a much improved resemblance with the LC population distribution pattern. The above described numerical test highlights the fact that the tuning of the Eulerian

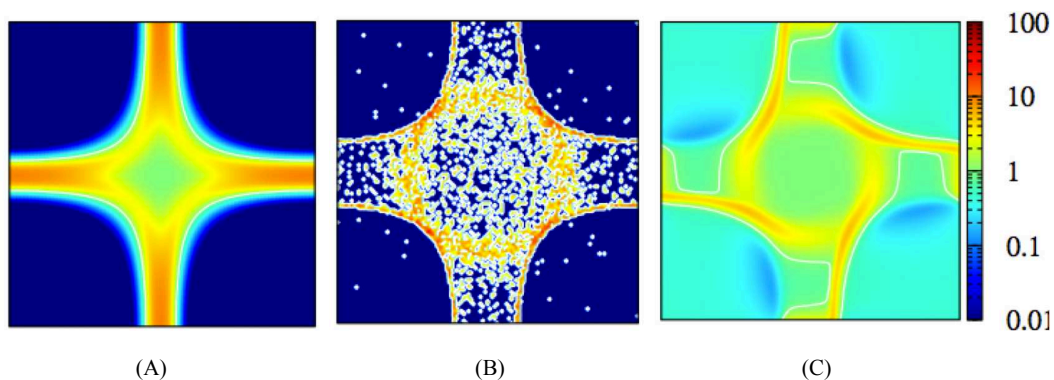


FIGURE 4 – Visualization in x-y plane of the normalised population density concentration  $C(x, y)/C_h$  in asymptotical steady-state regime in TGV flow.  $C(x, y)$  represents the local number density population concentration, while  $C_h$  is the same quantity corresponding to the homogenous distribution at initial time. The color-bar encode the  $C(x, y)/C_h$  excursions in logarithmic scale. Contour lines (white color) are traced at value of  $C(x)/C_h = 1$ . We compare the Lagrangian LC model (panel B) with Eulerian model results (panel A, C) at  $K_s = 0.01 U_0 L$  and respectively  $K_a = 130 U_0 L$  (A) and  $K_a = 1 U_0 L$  (C).

model on the Lagrangian one can be delicate. A difficulty lies in the way to treat the dependency of the diffusivity on the width term  $\delta\dot{\gamma}$ . A proper model tuning requires the quantity  $\delta\dot{\gamma}$  to be linked to the width of the transition in space ( $\delta x$ ) of the diffusivity  $\mathcal{K}$ . An idea for a possible improvement is here proposed.

First, the Taylor expansion of the strain-rate around the transition point between alert and safe regions ( $\mathbf{x}_T$ ) is written down :

$$\dot{\gamma}(\mathbf{x}) \simeq \dot{\gamma}_T + \nabla \dot{\gamma}|_{\mathbf{x}_T} \cdot (\mathbf{x} - \mathbf{x}_T). \quad (15)$$

Second, a rough estimate of  $\delta x$  is built on the dimensional estimate of the displacement produced by a jump,  $\delta x \simeq u_{JTJ}$ . Finally, combining these two approximations, one obtains the order of magnitude estimate  $\delta \dot{\gamma} = \|\nabla \dot{\gamma}|_{\mathbf{x}_T}\| \cdot \delta x = \|\nabla \dot{\gamma}|_{\mathbf{x}_T}\| u_{JTJ}$ . In conclusion, a better tuning for  $\delta \dot{\gamma}$  can be obtained through the evaluation of the norm of the gradient of the shear rate at the interface. While this approach seems to be feasible in the TGV flow, where  $\dot{\gamma}$  has an analytical expression as a function of position, it seems complicated to adapt it to turbulent flows (particularly in a higher spatial dimension).

A second caveat concerns the sensitivity of the model tuning to the functional form of  $\mathcal{K}(\dot{\gamma})$ . From eq. (11) and eq. (10), if we take into account that diffusivity is a function of  $\dot{\gamma}$  and the strain-rate in turn depends on space, then one can write

$$\Delta(KC) = K\Delta C + \frac{dK}{d\dot{\gamma}} (C\Delta\dot{\gamma} + 2\nabla\dot{\gamma}\nabla C) + \frac{d^2K}{d\dot{\gamma}^2} \left( (\nabla\dot{\gamma})^2 C \right). \quad (16)$$

In the case when  $C$  is chosen to be uniform, the terms contributing to the creation of the clustering are  $\frac{dK}{d\dot{\gamma}} (C\Delta\dot{\gamma})$  and  $\frac{d^2K}{d\dot{\gamma}^2} \left( (\nabla\dot{\gamma})^2 C \right)$ . This shows that the development of non-homogeneities is linked to the first derivative and to the second derivative of diffusivity with respect to  $\dot{\gamma}$ . Therefore, it seems that an accurate tuning of the Eulerian model is delicate and our choice of an hyperbolic transition shape for  $\mathcal{K}(\dot{\gamma})$ , eq (12), might not be an optimal one.

## 4 Conclusion

We conclude by underlying that the originality of the present study lies in its bottom-up approach : the experimental work and the associated data analysis was used to introduce an individual model for copepod dynamics. Such a model has been applied to the setting of small-scale oceanic turbulent flows and has allowed to suggest a mechanism for clustering of copepods in turbulence. Non-homogenous distribution of copepods has a key ecological importance particularly because it affects the encounter rates between organisms of the same kind and hence their reproduction. The negligible effect of the copepod orientational dynamics on the resulting spatial statistics implies that the dynamical properties of LC model can recast in terms of a space-time dependent diffusivity coefficient. Based on this observation a continuous Eulerian model has been proposed for the evolution of the population concentration of copepods. Preliminary encouraging results, based on a simple steady laminar flow have been shown. The problems connected to a proper tuning of the parameters of the continuous model have been discussed. The adaptation of the model to copepod populations in turbulent flows will be addressed in a future study.

*Acknowledgments* : The authors acknowledge support from European COST Action MP1305 ‘‘Flowing Matter’’ and the ‘‘GIP Seine-Aval ZOOGLOBAL project’’. We also thank Ibtissem Benkaddad for the experimental measurements, Dominique Menu and Regis Sion for technical support during experiments. H. A. has been supported by the PhD grant for interdisciplinary research ‘‘Allocation President 2013’’ of the University of Lille 1.

## Références

- [1] C. Razouls, F. de Bovée, J. Kouwenberg, N. Desreumaux, Diversity and Geographic Distribution of Marine Planktonic Copepods, Available at <http://copepodes.obs-banyuls.fr/en/index.php>, from 1883 to 2013/2014, (2017).
- [2] J. Jiménez, Oceanic turbulence at millimeter scales, *Scientia Marina*, 61 (1997) pp. 47-56.
- [3] B. R. MacKenzie, W. C. Leggett, Wind-based models for estimating the dissipation rates of turbulent energy in aquatic environments : empirical comparisons, *Marine Ecology Progress Series*, 94 (1993) pp. 207-216.
- [4] T. Kiørboe, H. Jiang, S. P. Colin, Danger of zooplankton feeding : the fluid signal generated by ambush-feeding copepods, *Proceedings of the Royal Society B : Biological Sciences*, 277 (2010) pp. 3229-3237.
- [5] H. Jiang, T. Kiørboe, The fluid dynamics of swimming by jumping in copepods, *Journal of The Royal Society Interface*, 8 (2011) pp. 1090-1103.
- [6] T. Kiørboe, E. Saiz, A. Visser, Hydrodynamic signal perception in the copepod *Acartia tonsa*, *Marine Ecology Progress Series*, 179 (1999) pp. 97-111.
- [7] T. Kiørboe, A. Visser, Predator and prey perception in copepods due to hydromechanical signals, *Marine Ecology Progress Series*, 179 (1999) pp. 81-95.
- [8] C. B. Woodson, D. R. Webster, M. J. Weissburg, J. Yen, Response of copepods to physical gradients associated with structure in the ocean, *Limnology and Oceanography*, 50 (2005) pp. 1552-1564.
- [9] C. B. Woodson, D. R. Webster, M. J. Weissburg, J. Yen, Cue hierarchy and foraging in calanoid copepods : ecological implications of oceanographic structure, *Marine Ecology Progress Series*, 330 (2007) pp. 163-177.
- [10] D. R. Webster, D. L. Young, J. Yen, Copepods' Response to Burgers' Vortex : Deconstructing Interactions of Copepods with Turbulence, *Integrative and Comparative Biology*, 55 (2015) pp. 706-718.
- [11] T. Kiørboe, *A Mechanistic Approach to Plankton Ecology*, Princeton University Press, (2008).
- [12] E. J. Buskey, P. H. Lenz, D. K. Hartline, Escape behavior of planktonic copepods in response to hydrodynamic disturbances : high speed video analysis, *Marine Ecology Progress Series*, 235 (2002) pp. 135-146.
- [13] E. J. Buskey, D. K. Hartline, High-Speed Video Analysis of the Escape Responses of the Copepod *Acartia tonsa* to Shadows, *The Biological Bulletin*, 204 (2003) pp. 28-37.
- [14] H. Ardeshiri, Dynamics of copepods in Turbulent Flows, Lille 1 University of Sciences and Technologies, PhD dissertation, 2016.
- [15] H. Jiang, T. R. Osborn, Hydrodynamics of copepods : a review, *Surveys in Geophysics*, Kluwer Academic Publishers, 25 (2004) pp. 339-370.
- [16] H. Jiang, G. A. Paffenhofer, Hydrodynamic signal perception by the copepod *Oithona plumifera*, *Marine Ecology Progress Series*, 373 (2008) pp. 37-52.
- [17] T. Kiørboe, A. Anderson, V. J. Langlois, H. H. Jakobsen, Unsteady motion : escape jumps in planktonic copepods, their kinematics and energetics, *Journal of The Royal Society Interface*, 7 (2010) pp. 1591-1602.

- [18] J. Yen, D. M. Fields, Escape response of *Acartia hudsonica* (Copepoda) nauplii from the flow field of *Temora longicornis* (Copepoda), *Ergebn. Limnol.*, 36 (1992) pp. 123-134.
- [19] P. H. Lenz, A.E. Hower, D. K. Hartline, Force production during pereopod power strokes in *Calanus finmarchicus*, *Journal of Marine Systems*, 49 (2004) pp. 133-144.
- [20] L. A. Duren, J. J. Videler, Escape from viscosity : the kinematics and hydrodynamics of copepod foraging and escape swimming, *Journal of Experimental Biology*, 206 (2003) pp. 269-279,
- [21] H. Ardeshiri, I. Benkaddad, F. G. Schmitt, S. Souissi, F. Toschi, E. Calzavarini, Lagrangian model of copepod dynamics : Clustering by escape jumps in turbulence, *Physical Review E*, 93 (2016), pp. 043117.
- [22] H. Ardeshiri, F. G. Schmitt, S. Souissi, F. Toschi, E. Calzavarini, Copepods encounter rates from a model of escape jump behaviour in turbulence, submitted to *Journal of Plankton Research*, preprint on Arxiv : <https://arxiv.org/abs/1702.03318> (2017).
- [23] M. R. Maxey, J. J. Riley, Equation of motion for a small rigid sphere in a nonuniform flow, *Physics of Fluids*, 26 (1983) pp. 883.
- [24] G. Jeffery, The Motion of Ellipsoidal Particles Immersed in a Viscous Fluid, *Proceedings of the Royal Society of London. Series A*, 102 (1992) pp. 61-179.
- [25] F. G. Michalec, S. Souissi, M. Holzner, Turbulence triggers vigorous swimming but hinders motion strategy in planktonic copepods, *Journal of The Royal Society Interface*, 12 (2015) 20150158.
- [26] F. De Lillo, M. Cencini, W. M. Durham, M. Barry, R. Stocker, E. Climent, G. Boffetta, Turbulent Fluid Acceleration Generates Clusters of Gyrotactic Microorganisms, *Physical Review Letters*, 112 (2014), 044502.
- [27] N. G. Van Kampen, *Stochastic processes in physics and chemistry*, Elsevier Science & Technology Books, (2007).
- [28] I. Siekmann, M. Bengfort, H. Malchow, Invasion patterns in competitive systems, Arxiv preprint, (2017).
- [29] A. W. Visser, U. H. Thygesen Random motility of plankton : diffusive and aggregative contributions *Journal of Plankton Research*, 25 (2003) pp. 1157-1168.
- [30] T. H. Solomon, J. P. Gollub, Chaotic particle transport in time-dependent Rayleigh-Benard convection, *Physical Review A*, 38 (1988) pp. 6280-6286