Predator-prey encounters in turbulent waters

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With reference to studies of predator-prey encounters in turbulent waters, we demonstrate the feasibility of an experimental method for investigations of particle fluxes to an absorbing surface in turbulent flows. A laboratory experiment is carried out, where an approximately homogeneous and isotropic turbulent flow is generated by two moving grids. The simultaneous trajectories of many small neutrally buoyant polystyrene particles are followed in time. Selecting one of these to represent a predator, while the others are considered as prey, we obtain estimates for the time variation of the statistical average of the prey flux into a suitably defined "sphere of interception." The variation of this flux with the radius in the sphere of interception, as well as the variation with basic flow parameters is well described by a simple model, in particular for radii smaller than a characteristic length scale for the turbulence. Also the Eulerian counterpart of the problem has been analyzed, and the particle fluxes from the two studies compared.

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Often the problem of turbulent diffusion in neutral turbulent flows is analyzed in terms of an initial value problem [1,2]. However, for many applications, a boundary-value problem is more relevant. As such an example we consider here the turbulent particle flux to an absorbing spherical surface. The problem serves, for instance, as a model for predator-prey encounters in turbulent waters, and seems to be one of the applications of the problem that has received most attention recently. For small predators, fish larvae for instance [3], it can safely be assumed that their self-induced motion is small or negligible, and that they are passively convected by the local flow velocity, at least to a good approximation. Similarly, it can be assumed that their food (microzooplankton, for instance) is also passively convected by the same flow. The feeding process can be modeled by assuming that any individual prey entering a suitably defined "sphere of interception" is captured with certainty. In turbulent waters, the predator-prey encounter rate is related to the problem of relative diffusion, but now considered as a boundary-value problem, with the condition that the prey concentration vanishes at the surface of the sphere of interception. This is the standard model for this particular problem [4–6]. The general interest in the problem arises essentially from the simple observation that the food concentration in the near region of a predator will rapidly be depleted, and without any self-induced motion a predator will be starving, unless the prey within its sphere of interception is replaced by turbulent motions in the flow. Here, we propose and demonstrate the feasibility of an experimental method for a statistical analysis, and present results for varying parameters.

The problem of predator-prey encounter rates has been studied in controlled laboratory experiments [7], and also by numerical simulations [8]. The basic features of the present experiment are described elsewhere [9], with a detailed description found in [10]. The turbulence is generated by the motion of two plastic grids, in the top and bottom of a tank with $320\times320\times450$ mm^3 inner dimensions. The motions of small polystyrene particles of size $d=0.5$–0.6 mm are followed with 4 video cameras, and the simultaneous positions of typically 500–1000 particles recorded at time intervals of 1/25 s. By a tracking procedure it is then possible to link the positions of particles, and thus follow their individual motions in three spatial dimensions, and in particular also to deduce their time varying velocity. It is ensured that the particles used in the experiment are neutrally buoyant. The average distance between particles is much larger than their diameter, and particle interactions can be ignored. To the given accuracy, we assume that the particles follow the flow as passive tracers [7,11].

Since the records for simultaneous particle trajectories are available, we can now select one to represent the predator and label all the others as prey. We then select a predetermined radius $\mathcal{R}$ in the sphere of interception, and remove all the particles which happen to be inside this sphere. During the subsequent Lagrangian motion of the reference "predator," we count the number of prey entering its comoving sphere of interception between successive time steps. Each time a particle enters, it is "eaten" in the sense that it is removed from the database. Of course, if the experiment is carried out for long times, all particles representing prey will eventually be removed. Here we are only interested in the time evolution of the prey flux for times up to an eddy turn over time. As long as $\mathcal{R}$ is much smaller than the size of the measuring volume, we can with negligible error assume the prey concentration to be constant at large distances, corresponding to ideally infinite systems. By choosing a large number of realizations, we can give an estimate for the ensemble averaged Lagrangian prey flux after time of release.

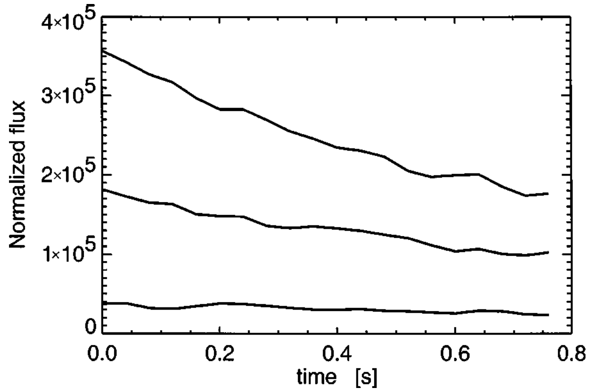

FIG. 1. Time variation of the estimate for the ensemble averaged particle flux for unit density $\langle J(t)\rangle/\eta_0$, to spheres with three different radii, $\mathcal{R}=15$, 30, and 45.

Experiments are carried out for different intensities of the turbulent velocity fluctuations, $\langle v^2\rangle$. With the polystyrene particles acting as markers for the local flow velocities, experimental estimates for the power spectrum for the fluctuations in velocity can be determined [9]. It was found that these power spectra can be modeled by

$$E(k)=\alpha\epsilon^{2/3}L^{5/3}\frac{(Lk)^4}{[1+(Lk)^2]^{17/6}} \tag{1}$$

to a good approximation, with α being a universal numerical constant, and ϵ the mean rate of dissipation of specific kinetic energy. The expression (1) serves also to define L as a characteristic length scale, which will be referred to later on. The experimentally obtained velocity power spectrum contains the characteristic $k^{-5/3}$ Kolmogorov Oubokhov subrange in the limit of large wave numbers. For very large wave numbers, k, the model has to be completed by a viscous subrange, but these small scales are beyond our resolution limit. All parameters entering Eq. (1) can be determined experimentally [9]. For instance, for the case discussed in the following, we found $\langle v^2\rangle^{1/2}=19$ mm/s, $L=28$ mm, $\alpha\epsilon^{2/3}=56$ mm$^{4/3}$/s^2, and $\epsilon=225$ mm^2/s^3. For the Kolmogorov length scale $(\mu^3/\epsilon)^{1/4}$ (at times called the inner scale) we found 0.24 mm, which is smaller than our spatial resolution.

In Fig. 1 we show examples for the time varying particle flux to a self-consistently moving sphere of interception with a given radius $\mathcal{R}$. This flux is the result of a competition between on the one hand the depletion of polystyrene spheres labeled "prey" in the near vicinity of the reference particle, and on the other hand the inward flux of such particles due to the turbulent motions in the flow. In each realization, we divide the flux by the prey density for that appropriate realization, and the result thus represents the prey flux for unit density. For small radii, $\mathcal{R}<L$, we find that the flux level is almost constant in time. A decreasing trend becomes conspicuous as the radius is increased, and for $\mathcal{R}>L$ we find a significant flux reduction for times approaching the eddy turnover time, $\tau_F\equiv L/\langle v^2\rangle^{1/2}$.

The prey flux to a sphere of interception moving self-consistently with the flow has been modeled by, for instance,

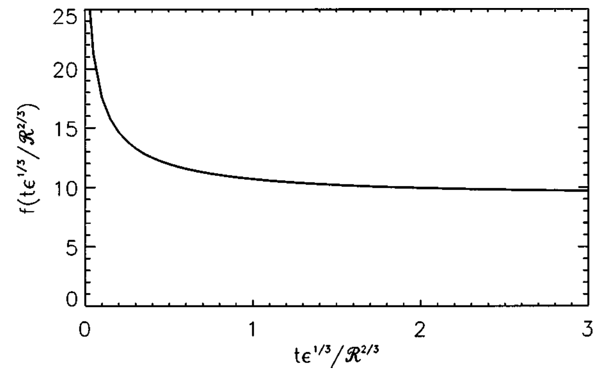

FIG. 2. Time variation of the normalized flux, $f(\tau=t\epsilon^{1/3}/\mathcal{R}^{2/3})$, obtained from Eq. (2), where distance is normalized by $\mathcal{R}$ and time by $\mathcal{R}^{2/3}/\epsilon^{1/3}$. The flux is then calculated to a sphere with unit radius. From the present result, we can derive the temporal flux variation for arbitrary $\mathcal{R}$ and ϵ by $J=\eta_0\epsilon^{1/3}\mathcal{R}^{7/3}f(t\epsilon^{1/3}/\mathcal{R}^{2/3})$. The (unphysical) singularity at $t=0$ is due to the assumed infinite initial gradient at $r=\mathcal{R}$. Note that the variation of $f(\tau)$ is rather slow for parameters relevant here, implying that the dominant parameter variations of the flux J are due to the coefficient.

a simple diffusion equation with a properly chosen diffusion coefficient which depends on the simultaneous mean-square velocity differences obtained at given spatial separations, but independent of time [6]. The equation proposed is actually identical to the one suggested by Richardson in his study of distance-neighbor functions [12]

$$\frac{\partial}{\partial t}n(r,t)=C\frac{\epsilon^{1/3}}{r^2}\frac{\partial}{\partial r}r^{10/3}\frac{\partial}{\partial r}n(r,t). \tag{2}$$

written for spherically symmetric geometry, with r being the radial coordinate, here taken from the position of the predator, and C the numerical constant, which is assumed to be universal. The derivations of Eq. (2) reported in the literature [6,12] assume that ϵ is a deterministic constant, and thereby ignore intermittency corrections [13]. Although the relation (2) had some experimental support from the time it was proposed [12] and also supported more recently [9], its validity has been criticized [1,2], see also the summary in [9]. The range of validity of Eq. (2) is not fully explored, keep in mind that for large separations a simple diffusion equation, with constant diffusion coefficient, is expected to apply, as indicated for instance by experimental results [14] for initial conditions having scales larger than the integral length scale. These two cases [9,14] referred to releases considered as initial value problems. It seems that a diffusion equation such as Eq. (2) can indeed be applied for analyzing relative two-particle diffusion in certain variable ranges [9], but it is well known, on the other hand, that one cannot expect that a diffusion coefficient depending solely on relative times or spatial separations is universally applicable for this problem [2].

From Eq. (2) is easy to derive [6] a steady-state flux to a sphere with radius $\mathcal{R}$ as $J=(28/3)\pi C\eta_0\epsilon^{1/3}\mathcal{R}^{7/3}$, where η_0 is the constant prey density at $r\to\infty$. In Fig. 2 we show a

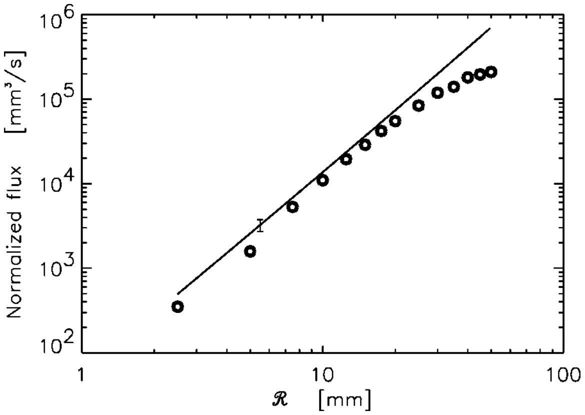

FIG. 3. The prey flux measured at 1/2 eddy turnover time, $t=\frac{1}{2}\tau_F$, to a given sphere of interception is shown with open circles for different radii. The full line gives the theoretical results from (2). Parameters are $\langle v^2\rangle^{1/2}=19$ mm/s, $L=28$ mm, $\tau_F=1.6$ s, and $\epsilon=225$ $\mathrm{mm}^2/\mathrm{s}^3$. The fluxes are normalized to unit density. An error bar on the curve gives the uncertainty due to C. The size of the symbols gives approximately the uncertainty on the measured points.

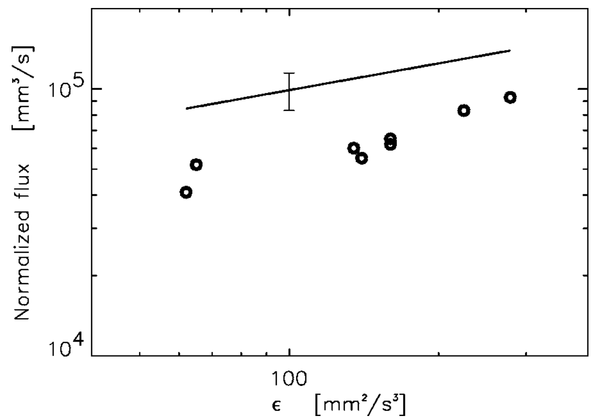

FIG. 4. Variation of the normalized flux with varying ϵ for a fixed value of $\mathcal{R}=25$ mm. The measured points are obtained at a time $t=\frac{1}{2}\mathcal{R}^{2/3}/\epsilon^{1/3}$. The full line gives the theoretical results obtained from Eq. (2). See also Fig. 3.

numerical solution of the normalized Eq. (2). More generally it can be argued by purely dimensional reasoning that the turbulent flux for unit density must have the form $J/\eta_0=\epsilon^{1/3}\mathcal{R}^{7/3}f(t\epsilon^{1/3}/\mathcal{R}^{2/3})$, with f being a dimensionless function of a dimensionless variable. The physical dimension of J/η_0 is *length*^{3}/*time*. With viscosity being immaterial for the flow dynamics for scale lengths larger than the Kolmogorov length scale $(\mu^3/\epsilon)^{1/4}$, we only have one quantity characterizing the turbulence, namely, ϵ with dimension *length*^{2}/ *time*^{3}, and the length scale $\mathcal{R}$ characteristic for the particular problem. Out of these, the only combination giving a quantity with dimension *time* is $\mathcal{R}^{2/3}/\epsilon^{1/3}$, while $\epsilon^{1/3}\mathcal{R}^{7/3}$ gives *length*^{3}/*time*. The actual form of f, including a numerical constant, can here only be determined by a numerical solution as shown in Fig. 2, where we used the value $C=0.32\pm0.05$ derived from the experimental results [9,10].

The experimental uncertainty on a particle position [10] is approximately 0.02 mm, and the idealized step function in prey density assumed as an initial condition when obtaining Fig. 2 is, therefore, not an exact representation for our experimental conditions. We, therefore, choose an illustrative time to be at a later stage, where the initial singularity in the solution in Fig. 2 no longer has any consequence.

In order to compare our observations with analytical results, we show by open circles in Fig. 3, the flux value at a time $t=(1/2)\tau_F$, with τ_F being the eddy turnover time. The corresponding analytical curve from Eq. (2) is shown by a full line. Taking into account that we have not introduced any free or adjustable parameters, we find that the agreement between the analytical and experimental results is satisfactory, although we find a slight, but systematic, reduction of the measured flux as compared to the analytical result. We note that the model equations become inadequate for spatial separations larger than the largest eddies in the turbulence, $r\geqslant L$, although we find that the $\mathcal{R}^{7/3}$ scaling seems to have a wider range of validity (in particular) at early times, $t<(1/2)\tau_F$.

We also present results for the flux variation for a fixed value of the radius of interception, $\mathcal{R}=25$ mm, and varying ϵ, see Fig. 4. The data are presented for a selected time $t=(1/2)\mathcal{R}^{2/3}/\epsilon^{1/3}$, and the theoretical ϵ variation is shown with a full line. Within the range of variability, we find the scaling for ϵ^a with $0.3<a<0.6$, which accommodates the theoretical value $a=1/3$. The numerical agreement between the measurements and analytical results is better than a factor of 2, the analysis predicting a slightly larger flux, also in agreement with Fig. 3. The selected value $\mathcal{R}=25$ mm can be taken as representative for the length scales smaller than or equal to L in the experiments.

Finally we note that the turbulent flux to a moving predator can be significantly smaller than the flux to a stationary one. This can be argued by noting that the relative mean-square velocity of a prey convected past a stationary predator is $\langle v^2\rangle$, while it is $\langle[\mathbf{v}(\mathbf{r},t)-\mathbf{v}(\mathbf{r}+\mathbf{y},t)]^2\rangle$, for a passively convected predator-prey pair, with separation $\mathbf{y}$. For small separations, $y\ll L$, we have [6] that $\langle[\mathbf{v}(\mathbf{r},t)-\mathbf{v}(\mathbf{r}+\mathbf{y},t)]^2\rangle\approx C'\epsilon^{2/3}y^{2/3}$ where C' is a constant, and the relative velocity is small, implying a small flux to the passively convected predator. For large separations, $y\gg L$, on the other hand, $\mathbf{v}(\mathbf{r},t)$ and $\mathbf{v}(\mathbf{r}+\mathbf{y},t)$ can be supposed to be statistically independent, and the mean-square relative velocity is then $2\langle v^2\rangle$. The flux in this latter case is expected to be larger than to a stationary predator, although such large separations cannot be achieved for the present experimental conditions.

The flux to a stationary predator can be analyzed in much the same way as we investigated the flux to a moving predator, although of course in this latter case we choose a fixed reference position, without requiring the presence of a polystyrene sphere in the center. We can define a "gain factor" as the ratio between the flux to a stationary predator divided by the flux to the passively convected predator with the same sphere of interception. In Fig. 5 we show this gain factor for various radii $\mathcal{R}$. All points are obtained at the reference time $(1/2)\tau_F$ used before. We find that the gain in prey flux achieved for a small predator, given the possibility of being anchored at a fixed position in the flow, is considerable for

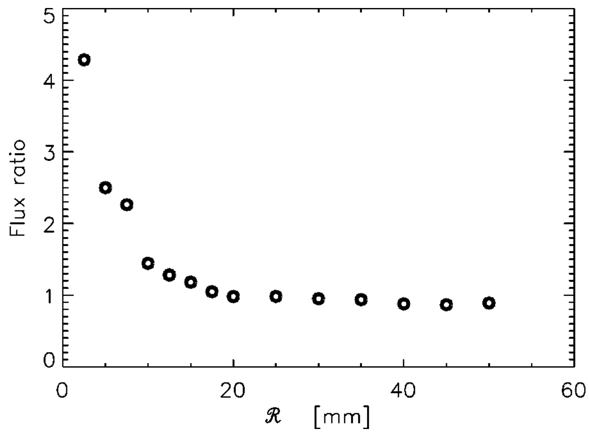

FIG. 5. Variation of the gain factor for a stationary predator for various radii in the sphere of interception, $\mathcal{R}$. The figure refers to a time $t=\frac{1}{2}\tau_F$.

small spheres of interception, using the length scale L as a measure. For $\mathcal{R}\approx L$ this gain factor is close to 1, and the prey flux is the same for a stationary as for the moving predator. For larger values $\mathcal{R}>L$ the flux to a moving predator exceeds that experienced by a stationary one. Seen from this point of view, it is clearly a disadvantage for a small predator to be passively carried with the turbulent flow, and our Fig. 5 quantifies this disadvantage.

In this correspondence we investigated the turbulent flux to a perfectly absorbing surface, with particular attention to the problem of predator-prey encounters in turbulent flows. We summarized the basic elements of an experimental method for investigating the prey flux to a moving predator. In the limit of small $\mathcal{R}$, we found evidence for an $\mathcal{R}^{7/3}$ flux scaling (see Fig. 3) in terms of the radius in a sphere of interception, and also found indications of an $\epsilon^{1/3}$ scaling with the turbulent dissipation rate (see Fig. 4), in agreement with the predictions of a model Eq. (2). This model also agrees quantitatively to some extent with the observations. We suppose that the observations justify extrapolation to radii, $\mathcal{R}$, smaller than those experimentally accessible. We expect that in order to obtain a general model, which can give results for extended time periods and all $\mathcal{R}$, we will have to allow for a diffusion coefficient which depends on time as well as spatial separations, in particular, also including memory effects [2].

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