Plankton’s perception of signals in a turbulent environment

H. L. Pécseli a and J. K. Trulsen b

aPhysics Department, University of Oslo, Oslo, Norway; bInstitute of Theoretical Astrophysics, University of Oslo, Oslo, Norway

ABSTRACT
Aquatic micro-organisms often depend on detecting signals caused by motions in the surrounding flow. The antennae and setae of plankton are considered as examples of small fibers that here serve to detect variations in the local fluid velocities. It is argued that the noise induced by the turbulent environment can disturb the signals originating from moving prey or predators. At times, the turbulent noise can be mistaken to represent a signal, motivating erratic attack or escape responses. The present review addresses the latter problem. The analysis is kept on a level sufficiently simple to let the results have practical applicability, while on the other hand, the basic elements of the problem are retained. More generally, the results can be applied for estimating some of the effects of turbulence on small rigid fibers being transported by a turbulent flow. Known results are supplemented by new findings, extending the parameter range.

1. Introduction
Small particles or fibers are often found in a turbulent environment in a variety of industrial applications as well as in nature [1]. One example is fibers transported by fast and turbulent flows in paper industry [2]. The antennae of small organisms, plankton, can also be seen as small fibers, and these are influenced...
by a turbulent environment as well [3]. The present review will be concerned mostly with the latter problem.

The survival of marine zoo-plankton relies on detection of signals in their near fluid environment, to identify either prey or predators. The surroundings are, however, seldom quiet. Winds, tides, and currents generate turbulent motions that can in some cases be a disadvantage, in other cases advantageous. It has thus been suggested [4–7] that turbulent mixing in the environment can bring predators and prey close from time to time, and thereby enhance the probability of capture even without relying on self-induced motions. A number of observations support these ideas [8–11]. A laboratory experiment with tiny polystyrene spheres representing predators and prey confirmed basic analytical scaling laws for turbulence-induced encounter rates [12]. Low levels of turbulence are thus advantageous for predators by enhancing the contact rate of prey. It was, however, also argued that very large turbulence levels enhance the relative motions between predator and prey to make the time available for capture small. Hence, the capture probability is reduced in this limit [13–17]. Due to a competition between these two effects, there will be an optimum level of turbulence for predation. In general, it will be different for different species.

Turbulence can also have effects on plankton’s perception of and reaction to the surroundings. Many organisms thus depend on sensing motions in their fluid environment both for detecting prey and for identifying predators. In a quiet environment, the process can be unambiguous, but in the presence of turbulence, a signal detected by the antennae of plankton (see Figure 1) can become difficult to interpret: the turbulence acts as noise, masking or even dominating the signal. Observations [18] indicate that plankton can experience and react to such ‘noise effects.’ Observing the feeding and swimming behavior of freely swimming cod (Gadus morhua) and herring larvae (Clupea harengus) in calm and turbulent laboratory environments at limiting and satiating abundances of Acartia tonsa prey, it was found that attack position rates were significantly higher in turbulent than in calm water at low food abundances for two size groups of cod [19]. The copepod Acartia clausi has been observed to increase the number of escape reflexes in response to enhanced turbulence levels [10]. In those studies, the observed escape reactions did not seem to have any other motivation than the turbulence.

In the present study, we will discuss means for quantifying the turbulent noise. A complete analysis will require knowledge of the entire flow field at and in the vicinity of the organism and the coupling of the flow to the sensory organs through the viscous layer at the body [20,21]. Even if all this information was available, the results would be long and unhandy. It is, however, possible to reduce the problem to some basic elements. With this starting point we can use results from signal analysis [22,23] to quantify the noise in such a way that the results appear in a compact and useful way. At the same time, the basic elements of the problem are retained to sufficient accuracy. Some of the basic statistical
information needed has not been obtained before and are presented here for the first time. In standard signal analysis, it can often safely be assumed that the noise is a Gaussian random process with relatively simple analytical forms available for predicting basic characteristics, in particular also joint probability densities. For incompressible neutral turbulence, it turns out that intermittency effects make models derived from a strictly Gaussian random processes inadequate, and we have to obtain the relevant statistical information experimentally or numerically. Fortunately, high-resolution numerical simulations are available for this [24,25].

The present problem is interesting also by its cross-disciplinary nature: it contains elements of marine biology, fluid mechanics, numerical simulations, and signal analysis.

2. Analysis

The analysis can logically be separated into three parts: (1) a description of the turbulent flow environment, (2) a parametrization and modeling of the signal detected by the organisms, and finally (3) a parametrization and modeling of the disturbing noise caused by the turbulent environment.

2.1. The turbulent environment

Typical turbulence parameters found in nature [16,28] are summarized in Table 1. An effective Kolmogorov scale $\eta_0$ is introduced [15]: it is defined as the range where a dissipation range structure function merges with the structure function characterizing the inertial range. We have $\eta_0$ being approximately one order of magnitude larger than the classical Kolmogorov scale $\eta \equiv (v^3/\epsilon)^{1/4}$. 
Table 1. Turbulence parameters encountered in the oceans. The kinematic viscosity is taken as \( \nu = 0.89 \text{ mm}^2 \text{ s}^{-1} \). In general the viscosity depends on salinity and temperature.

| Location      | Specific energy dissipation rate | Modified Kolmogorov length | Kolmogorov time \( \tau_K \) |
|---------------|---------------------------------|----------------------------|----------------------------|
| Open ocean    | \( \epsilon \sim 10^{-4} - 1 \text{ mm}^2 \text{ s}^{-3} \) | \( \eta_0 \sim 130 - 13 \text{ mm} \) | \( \tau_K \sim 100 - 1 \text{ s} \) |
| Shelf         | \( \epsilon \sim 10^{-1} - 1 \text{ mm}^2 \text{ s}^{-3} \) | \( \eta_0 \sim 26 - 13 \text{ mm} \) | \( \tau_K \sim 3.0 - 1 \text{ s} \) |
| Coastal zone  | \( \epsilon \sim 10^{-4} - 10^2 \text{ mm}^2 \text{ s}^{-3} \) | \( \eta_0 \sim 26 - 2.6 \text{ mm} \) | \( \tau_K \sim 3.0 - 0.1 \text{ s} \) |
| Tidal front   | \( \epsilon \sim 10 \text{ mm}^2 \text{ s}^{-3} \) | \( \eta_0 \sim 6.5 \text{ mm} \) | \( \tau_K \sim 0.3 \text{ s} \) |

For many purposes, this distinction would have only minor consequences, but in the oceans, it turns out that scale sizes of plankton are close to \( \eta \) and the more accurate expressions can become important to distinguish whether turbulence models for the viscous or for the inertial subrange should be applied.

2.2. Parametrization of the signal detected by plankton

Prey or predator passing plankton induces velocity variations along its antennae and setae, as illustrated in Figure 1. Plankton is capable of sensing even minute velocity variations in the flow surrounding its antennae. Studies of *Labidocera* [26,29] demonstrated that their large spike receptor may be considered as a relative velocity detector, requiring only a 20 \( \mu \text{m} \text{ s}^{-1} \) velocity difference of the fluid across setae (see Figure 1) to trigger a neural response. Other related studies [27] indicate that larger flow velocities are needed for a larger organism (*Gaussia princeps*). These values will be used as representative indicators for plankton sensitivity, but there is a noticeable scatter in sensitivity for different species. Some studies [26,30,31] indicate that velocity variations less than 100 \( \mu \text{m} \text{ s}^{-1} \) can elicit attack, although these values depend on orientations, light conditions, etc. Other related studies can be found in qualitative support of these results [32].

Figure 1 uses a copepod for a schematic illustration. It is, however, a generally valid conclusion that plankton can be considered neutrally buoyant and moving at low Reynolds numbers, and reacting to flow differences rather than absolute velocities. More generally, we let \( b \) in Figure 1 denote a characteristic size of the flow velocity sensing organs for plankton.

The basic characteristics of the detected fluctuations are their amplitudes, but also the duration of a pulse can play a role in the interpretation. Plankton is thus able to distinguish slow and fast signal variations having the same peak amplitudes and react selectively to hydrodynamic disturbances [21,33,34].

A single receptor or seta will give a response in proportion to a velocity component perpendicular to its direction and therefore have limited directional sensitivity. The full information of the velocity vector requires a three-dimensional distribution of setae (very similar to a sonic anemometer). Even such a configuration gives only a direction and not a distance to the disturbance causing the velocity variation. This full information requires two or more receptors, increasing separation giving increasing directional sensitivity. Here, we consider signals from the two ends of the antennae with separation \( b \) in Figure 1 as
representative. Two limiting cases are considered, (a) one where the disturbance originates form a large distance, $p \gg b$ and (b) one where $p \ll b$. Only velocity differences are important here: a large-scale velocity variation moves the entire organism and no velocity differences appear along the setae.

As a reference case, we consider prey moving with velocity $U$. Depending on details in the prey propulsion [35], we find that the strength of the velocity perturbation induced by moving prey scales as $AU/r^m$ with distance $r$, for motions at low Reynolds numbers. The exponent $m$ characterizes how rapidly the velocity disturbance decays away from the organism, while $A$ is a dimensional parameter depending, for instance, on the size and shape of the organism; typically, we have $m = 1 - 3$. For passive sinking or for the velocity field generated by a feeding current, we have $m = 1$ and $A \approx a$, the size of the organism. For a self-propelled organism, we find $m = 2$ and $A \approx a^2$ [35]. In case (a), we argue that as an order of magnitude the detected velocity difference between sensors at the two ends of the antenna $b$ in Figure 1 is

$$v_p(t) \approx AU \left( \frac{1}{r_0^m(t)} - \frac{1}{r_b^m(t)} \right).$$

A more accurate and detailed expression will depend on relative orientations of the organisms, the angle between the vector $U$ in Figure 1 and the antenna $b$, together with other geometrical parameters. For the particular case with a head-on encounter, the velocity differences over the antenna will not be detected since the bulk velocity variation will merely displace the entire copepod in Figure 1. The expression given before assumes an average over parameters specifying the details of individual encounters.

An order of magnitude estimate of characteristic time durations of perturbations is $\tau_p \sim p/U$, apart from a numerical constant that depends also on $m$. The impact parameter $p$ determines the closest distance between predator and prey with the given motion. For case (a), when $p \gg b$, we can use the order of magnitude estimate for the peak value of the velocity disturbance by the approximations $1/r_0^m \approx 1/(p - \frac{1}{2}b)^m \approx (1 + \frac{m}{2}b/p)/p^m$ and $1/r_b^m \approx 1/(p + \frac{1}{2}b)^m \approx (1 - \frac{m}{2}b/p)/p^m$, giving

$$v_{\text{max}} \sim \frac{mbAU}{p^{m+1}}. \quad (1)$$

It is an advantage for a predator as well as prey to have a ‘stealth capacity,’ where the disturbances in the flow decay rapidly with distance. This is achieved for large $m$-values. For breast stroke swimmers such as Mesodinium rubrum, Acartia tonsa, and Podon intermedius, the flow disturbances have been measured by use of particle image velocimetry to decay as one over distance cubed [36], i.e. $m = 3$. On the other hand, an increased $m$-value will for most relative orientations give
rise to a larger variations in the velocity components along the antennae, making it easier to identify the direction to the origin of the fluid velocity disturbance.

In the other limit, case (b) with $p \ll b$, we have $u_0 \approx 0$ and $u_b \approx U$. It can then safely be assumed that the detected velocity difference is simply proportional to $U$ and the duration of the disturbance can be approximated as the time it takes the organism of scale size $a$ to pass the nearby antennae, i.e. $\tau_p \approx a/U$.

Plankton is characterized by a large variety of motion strategies and motion velocities that depend on the species considered, their age etc., but also on the local environment. Travel speeds will be small compared to attack or escape velocities, that are often an order of magnitude larger. Large databases containing relevant information have been compiled [37]. As an illustrative order of magnitude estimate for travel speeds for case (a), we can take $U \approx 1 \text{ mm s}^{-1}$, $p \approx 10 \text{ mm}$ and find $\tau_p \approx 10 \text{ s}$. To estimate the maximum velocity difference perturbation $\nu_{\text{max}}$, we assume that the organism moving in a quiet environment induces a velocity perturbation of $\sim 1 \text{ mm s}^{-1}$ at a distance $p$, meaning that $AU/p'' \approx 1 \text{ mm s}^{-1}$. This estimate gives $\nu_{\text{max}} \approx (mb/p) \times 1 \text{ mm s}^{-1}$. With $m = 2$ and $b \approx 5 \text{ mm}$, these arguments give $\nu_{\text{max}} \approx 1 \text{ mm s}^{-1}$ which is larger than the minimum detectable velocity variations observed [26,27,30,31]. For case (b), we can take $a \approx 5 \text{ mm}$ and $U \approx 1 \text{ mm s}^{-1}$ to find $\tau_p \approx 5 \text{ s}$ which is similar to the value found for case (a). For order of magnitude estimates, the two cases can be treated at the same level.

The two characteristics, the maximum velocity perturbation $\nu_{\text{max}}$, and the characteristic time scale $\tau_p$ for perturbations induced by moving prey or predators have to be compared to perturbations, induced by turbulence in the surrounding flow.

### 2.3. Parametrization of the turbulence-induced noise

The turbulent velocity variations will be described by the statistics of the velocity differences $\nu(r, t) \equiv (u(r_a + r, t) - u(r_a, t)) \cdot \hat{r} = u_\parallel(r_a + r, t) - u_\parallel(r_a, t)$ where $\hat{r} = r/r$ for some separation distance $r$. For homogeneous stationary turbulence, the statistical averages will be independent of $t$ and $r_a$. The choice for the scalar $\nu$ is restrictive by emphasizing only the longitudinal velocity components [38], but the statistical information, for instance, of the transverse component can be derived from the results for the longitudinal velocity [38,39].

The basic statistical information is contained in the amplitude probability density $P(\nu)$. This information does not, however, contain all that is needed: we can find the probability for the signal amplitude to exceed a certain level, but we will not know how frequently this happens, nor do we know the duration of time the signal exceeds the selected level after an upward crossing to the next downward crossing. This information can be found, or at least estimated, once we know the joint probability density $P(\nu, \nu')$ for $\nu(t)$ and its time derivative $\nu'(t) \equiv d\nu/dt$ [22,23]. The arguments for deriving the most relevant statistical averages are summarized in the following [3].
For time stationary random processes $\nu(t)$, the expected or average number of crossings $d\langle N(U_\ast) \rangle$ of a selected level $U_\ast$ in a time interval $dt$ is equal to the ratio of (i) the expected amount of time spent in the interval $d\nu$ for a given $d\nu'$ in a time interval $dt$, and (ii) the deterministic time interval $\tau \equiv d\nu/d\nu'$ required to cross the interval $d\nu$ for a given $\nu'$. This is a special case of a general theorem addressing stationary random processes [22,23]. After some simple manipulations, the ratio of (i) and (ii) is found to be

$$\frac{P(\nu, \nu') d\nu d\nu' dt}{d\nu/d\nu'} = \nu' P(\nu, \nu') d\nu' dt. \quad (2)$$

The average frequency $d\langle N(U_\ast) \rangle/dt$ of upward crossings of a selected level $\nu = U_\ast$, irrespective of the magnitude of the signal derivative $\nu'$ at the time of crossing, is then obtained from (2) by integration with respect to all positive $\nu'$ to give

$$\frac{d\langle N(U_\ast) \rangle}{dt} = \int_0^\infty \nu' P(U_\ast, \nu') \, d\nu'. \quad (3)$$

The detected fluctuating velocity difference over the antennae at the associated level crossings are interpreted as an ‘error signal’ in the sense that it does not represent the presence of prey or a predator. The energy dissipation $\epsilon$ enters implicitly through $P(U_\ast, \nu')$: in particular, it is not correct simply to assume the error signal or ‘noise’ to be proportional to $\epsilon$ [16].

To supplement the information of the average level crossing frequency, we take an estimate for the average duration $\langle T \rangle$ from an upward to the first following downward crossing of the selected level. A complete analysis turns out to be complicated [22]. A simplified approximate expression can however be found. For stationary random noise, it can be argued [40,41] that this time can be estimated (note that this is not an exact analytical result) by the average time spent above a reference level divided by the average number of upward crossings. The result is

$$\langle T(U_\ast) \rangle = \frac{\int_{U_\ast}^\infty P(\nu) \, d\nu}{\int_0^\infty \nu' P(U_\ast, \nu') \, d\nu'} \quad (4)$$

For large negative $U_\ast$, we have that all of the time is spent above the reference level so $\langle T(U_\ast) \rangle$ is diverging for $U_\ast \to -\infty$. The results (3) and (4) are consistent in the sense that $d\langle N(U_\ast) \rangle/dt < 1/\langle T(U_\ast) \rangle$ for all $U_\ast$. The expression (4) has been tested using synthetic data series [42]. In the limit of a Gaussian random signal, it produces near exact results, so the expression can be used with confidence in the general case.

### 3. Results

The results for $d\langle N(U_\ast) \rangle/dt$ and $\langle T(U_\ast) \rangle$ can be obtained once the joint probability density $P(\nu, \nu')$ is known. Unfortunately, no analytical study or experimental results are available for this. Here, we obtain an estimate for $P(\nu, \nu')$ by use of
results from numerical simulations \[24,43\]. Two data-sets from large numerical simulations of incompressible turbulence are available with significantly different parameters. The two databases are described elsewhere \[43,44\]. The largest one has a spatial resolution of \(1024^3\) with 1841 time steps, the smaller one has a resolution of \(512^3\) with 1167 time steps, both with periodic boundary conditions with box size \((0, 2\pi)\). They are in the following referred to as the large and small data-set. The entire space-time varying three-dimensional flow field contains too much information for practical storage. The available database consists of the trajectories (positions and velocities as functions of time) of \(\sim 10^5\) point particles moving with the flow in the large data-set. Concerning simulation parameters, the largest difference can be found in the simulation viscosity parameters \(\nu = 8.8 \times 10^{-4}\) and \(2.05 \times 10^{-3}\), respectively, in computational units. The data analysis is carried out by choosing a separation distance and then obtaining histograms of the velocity differences and velocity difference derivatives of particles separated by the chosen length within a narrow interval. Given the large database, these histograms will give good approximations for the probability densities of velocity differences, and the time derivatives. In particular, also the joint probability density for these quantities can be estimated.

It is a great advantage, when possible, to represent results in terms of scaled variables, i.e. normalized velocity differences such as \(v(r\epsilon)^{-1/3}\), etc. Otherwise, we would need separate curves for each choice of \(\epsilon\) and \(r\). For the present problem, it turns out to be possible to give such compact presentations as summarized in a number of figures. As a first step of the analysis, we illustrate the accuracy of this scaling and show in Figure 2 the velocity difference probability density corresponding to point separations in the viscous and inertial turbulent subranges, respectively. The mean square average for these two probability densities give \(1/12 r^2 \epsilon/\nu\) and \(C_K r^{2/3} \epsilon^{2/3}\), respectively, with \(C_K \approx 2.1\) being the universal Kolmogorov constant. These quantities can be interpreted as the mean square of the ‘noise’ experienced by plankton in a turbulent environment \[35\].

Figures 2 and 3 contain inserts to illustrate the difference between scaled and non-scaled presentations. Note in particular the horizontal axis in Figure 3(b) which does not contain the separation \(r\). Indeed, no \(r\)-variation is observed in the unscaled presentation. A dependence on \(\epsilon\) can, however, be noted.

We find that the two scalings or normalizations are satisfied to very good accuracy. Similar scalings are found for the statistical distribution of the time derivatives \(dv(t)/dt\) as shown in Figure 3. Deviations from a Gaussian model indicate intermittency effects \[45\]. A slight systematic difference between the results from the two data-sets can be noticed, but for the probability density estimates shown these differences are immaterial. Corresponding normalized joint probability densities are shown in Figure 4. We note that if we try to use wrong scaling laws, e.g. use inertial scalings for the viscous subrange and vice versa, the agreement is lost entirely.
Figure 2. Normalized probability densities for the longitudinal velocity differences obtained for separations $r$ in (a) the viscous ($r < \eta_0$) and (b) the inertial subranges ($r > \eta_0$) of the turbulence. Selected separations are $r = 0.010, 0.015, 0.020, 0.025, 0.030$ for the viscous and $r = 0.205, 0.255, 0.305, 0.355, 0.405, 0.455, 0.505$ for the inertial subranges, using computational units. The horizontal axes of the inserts have the variables on the top of the figure to save space. The two data-sets are indicated by full red and dashed black lines. Thin dash-dotted lines give the best Gaussian fits.

Figure 3. Normalized probability densities for the time derivatives of longitudinal velocity differences obtained for separations $r$ in (a) the viscous ($r < \eta_0$) and (b) the inertial subranges ($r > \eta_0$) of the turbulence. Selected separations $r$ and the figure layout is the same as in Figure 2.

Figure 4. Normalized joint probability densities for normalized $\nu(t)$ and $d\nu(t)/dt$ obtained for separations in the viscous (a) and inertial (b) subranges showing $P(\nu(r^2e/\nu)^{-1/2}, d\nu(t)/dt (r e/\nu)^{-1})$ and $P(\nu(r e)^{-1/3}, d\nu(t)/dt (e^3/\nu)^{-1/4})$, respectively.

By the information given in Figure 4, it is now possible to obtain estimates for $d\langle \mathcal{N}(U_s) \rangle/dt$ and $\langle \mathcal{T}(U_s) \rangle$ using the expressions (3) and (4). The integrations are done numerically. The results are shown in Figures 5 and 6. We show results
Figure 5. Normalized average level crossing frequency. Red curves are obtained for the larger one of the two data-sets, full black line is the smaller data-set, while the dashed line is the result for an equivalent Gaussian random process.

from the large and small data-sets individually with different color codes, also for illustrating the scatter in results from numerical simulations. The general trends, even in small details, are very similar, but we note a small offset between the two results. We have most confidence in results from the large data-set because of the better resolution of the viscous subrange. The effects of the 'bottleneck' effect are here strongly reduced. This effect is a feature found in many numerical simulations of turbulent flows [46,47]. Physically, the bottleneck effect arises because of the finite resolution of the sub-Kolmogorov scales, giving a lack of small-scale vortices, which makes the energy cascade less effective around the Kolmogorov scale, as compared to ideal, physical conditions. Results from the small data-set in Figures 5(a) and 6(a) have enhanced uncertainties due to a smaller database in the viscous limit. We find that the small differences in probability densities evident in, for instance, Figures 2 and 3 accumulate to give more conspicuous consequences here. It is also important to note that a Gaussian model is at most giving correct orders of magnitude. Intermittency effects are important for the problems analyzed here.

By inspection of Figure 6(a) and (b), we find that the average duration of positive excursions of the velocity difference $\nu(t)$ between base and tip of the antennae of a copepod will have typical durations of $10 \tau_K$ or less in both the viscous and inertial subranges. The zero-crossing frequencies are approximately $0.09/\tau_K$ and $0.05/\tau_K$ in the viscous and inertial subranges, respectively. The noise signal experienced in the viscous subrange is of a lower level but of a higher frequency compared to what is found for the inertial subrange. For large negative $U_*$, we have that all of the time is spent above the reference level so $\langle T(U_*) \rangle$ is diverging for $U_* \to -\infty$ in both Figure 6(a) and (b). To distinguish positive and negative values of the velocity differences, we need an additional figure that is not reproduced here. Estimates for $U_* < 0$ can use mirror images of Figure 6(a) and (b) to sufficient accuracy.
Figure 6. Estimate for normalized average duration of time interval between an upcrossing and the first successive downcrossing. Red curves are also here obtained for the larger one of the two data-sets, full black line is the smaller data-set, while the dashed line is the result for an equivalent Gaussian random process.

4. Applications of the results

To illustrate the use and applicability of the results summarized in Figures 5 and 6, we consider some specific examples.

(a) In the coastal zone and in the tidal front, we can find $\epsilon \sim 10 \text{ mm}^2\text{s}^{-3}$, giving a modified Kolmogorov length scale $\eta_0 \sim 6.5 \text{ mm}$ and a Kolmogorov time scale $\tau_K \sim 0.3 \text{ s}$. For an organism like, for instance, *Gaussia Princeps* with antennae $b \approx 10 - 15 \text{ mm}$ size [27], we use data relevant for the inertial subrange. Assume that we want to know how frequently, on average, the organism experience a turbulence-induced velocity difference across its antennae of $U_* \approx 1 \text{ mm s}^{-1}$. This is a relevant number for the signal induced by a moving predator or prey. We find the normalized value $U_*(b\epsilon)^{-1/3} \approx 0.25$. By Figure 5(b), we find that this corresponds to $\tau_K d\langle N(U_*) \rangle/\langle dt \rangle \approx 0.05$ giving for this case $d\langle N(U_*) \rangle/\langle dt \rangle \approx 0.17 \text{ s}^{-1}$, i.e. a ‘level crossing’ once every 6 s on average. From Figure 6(b), we find that the average duration of time before the noise level again falls below the selected $U_*$ is $9\tau_K \approx 3 \text{ s}$, which is of a magnitude that can be misinterpreted as a signal of moving predators or prey. If we consider conditions with four times larger $\epsilon$ which can be found in the coastal zones, see Table 1, the value of $\tau_K d\langle N(U_*) \rangle/\langle dt \rangle$ increases only little, but the Kolmogorov time scale becomes one half of the previous value so that $d\langle N(U_*) \rangle/\langle dt \rangle \approx 0.3 \text{ s}^{-1}$. In this environment, the turbulent noise can be dominating so that a proper identification of predators or prey becomes difficult. The motion strategies of copepods, also such as mate searching strategies, can be confused by turbulence [18].

(b) As an alternative, we can take conditions found frequently at the shelf, see Table 1, with $\epsilon \sim 1 \text{ mm}^2\text{s}^{-3}$ giving $\eta_0 \sim 10 \text{ mm}$ and $\tau_K \sim 1 \text{ s}$. With antennae lengths $b = 5 \text{ mm}$ in Figure 1, we need data for the viscous subrange. Taking again $U_* \approx 1 \text{ mm s}^{-1}$, we find the normalized value
$U_*(b^2 \epsilon/\nu)^{-1/2} \approx 0.2$. By Figure 5(a), we find $\tau_K d\langle \mathcal{N}(U_*) \rangle/dt \approx 0.06$ giving $d\langle \mathcal{N}(U_*) \rangle/dt \approx 0.06$ s$^{-1}$, i.e. approximately one level crossing per 15 s on average. By Figure 6(a), we find $\langle T(U_*) \rangle/\tau_K \approx 5$ giving here an average pulse duration of $\langle T(U_*) \rangle \approx 5$ s. This is a relatively long time that may be distinguishable from the signals induced by moving predators or prey. Turbulent noise will have a minor role in this environment.

These examples used a relatively large value for $U_*$ for illustration. Recall that even velocity variations below 0.1 mm s$^{-1}$ are detectable [48]. The examples are readily modified to account for smaller and even more realistic velocities. According to our results, the turbulent noise will make recognition of signals from predators or prey difficult for turbulence levels exceeding the maximum value shown in Table 1.

The present summary refers to average frequencies and durations of single or individual escape or attack events as those observed in studies of some fish larvae [10,19] as also discussed in the Introduction. If we consider a multitude of such events, they can contribute to the bulk displacement or diffusion of plankton by random walk [49]. Since the activity is enhanced in turbulent regions of the flow surrounding the organisms, this motion will on average give rise to a slow migration away from turbulent regions into calmer fluid environments.

5. Conclusions

We reviewed analytical methods for describing and quantifying the effects of turbulence that plankton experiences as noise in the environment. Known results [3,15,16,35] were extended and supplemented by new findings, mostly referring to the inertial subrange of turbulence. We provide some simple and directly applicable results that can be used for estimating the variability in the fluctuating signals experienced by the sensory organs of plankton. The noise is due to random turbulent motions in the surrounding flow. Due to some simple scaling laws, the results can be applied for a wide range of parameters encountered in the environment. The results summarized here represent solutions of an idealized problem, where we approximated the sensory responses by a velocity difference and by modeling the basic characteristics of the signals in terms of amplitudes and time durations. The results are amenable for laboratory tests [3].

The present study used the fluctuating scalar $\nu(t)$ obtained by the longitudinal velocity difference component [38]. For particle separation studies, this is the relevant component and is most often studied. It will be relevant also if elongations of small fibers is studied. The statistical information of, for instance, the transverse component can be derived from the results for the longitudinal velocity [38,39].

This review emphasized the effects of turbulence on predator–prey interactions. Turbulence also influences the mating strategies of plankton. In quiet laboratory environments, female copepods leave long traces of pheromones that
are faithfully followed by the male [50]. Even low levels of turbulence will dilute and distort such trails, necessitating a strategy taking into account the turbulent environment.

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**ORCID**

H. L. Pécseli [http://orcid.org/0000-0002-7122-9641](http://orcid.org/0000-0002-7122-9641)

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