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Oceanic turbulence at millimeter scales*

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SUMMARY: The basic theory of turbulence is reviewed, especially as it applies to the smallest scales, in the parameter range typical of the ocean above the thermocline but away from the direct effect of surface waves. The main time and length scales are defined, and related to the environment experienced by particles in the size range of plankton.Two problems are analysed in some detail to illustrate the application of the theory: the differential concentration of almost neutrally buoyant particles, and the size of the sensory and feeding horizon of current feeders.

Key words: Turbulence, dissipation range, plankton.

INTRODUCTION

Turbulence has been studied for more than a hundred years, since it was found that the friction losses in the pipes used in city sewerage became independent of velocity beyond a certain threshold (Hagen, 1854; Darcy, 1855). Soon after that, Boussinesq (1877) and Reynolds (1894) understood correctly that the properties of the new regime were due to random velocity fluctuations, which acted roughly as the thermal agitation of the molecules in a gas, and introduced an effective viscosity and diffusivity which were much larger than the molecular ones.

The experimental and theoretical understanding of turbulence developed steadily, culminating in Kolmogorov's (1941) prediction of the form of the energy spectrum. Even if, as we will see below, the theory that led to that prediction is only an approximation, it has been shown to be correct in the same sense as Newtonian physics; while we know that there are relativistic and quantum corrections to Newton's laws, and that those corrections enable such engineering applications as electronics and atomic energy, in most practical cases the errors are small and can be neglected.

Still, a full theory of turbulent flows eludes us. The main problem is our inability to make quantitative predictions. While we can compute some physical constants to ten significant digits, we cannot compute the drag of a sphere to within 10%. Most of the schemes used today to simulate turbulence hide adjustable parameters that can only be determined by comparing the calculations with experiments under conditions similar to those which are being computed. They are essentially clever, although physically motivated, interpolation schemes. The only exception is the direct numerical simulation of turbulent flows, in which the Navier-Stokes equations are integrated numerically without approximation, but its

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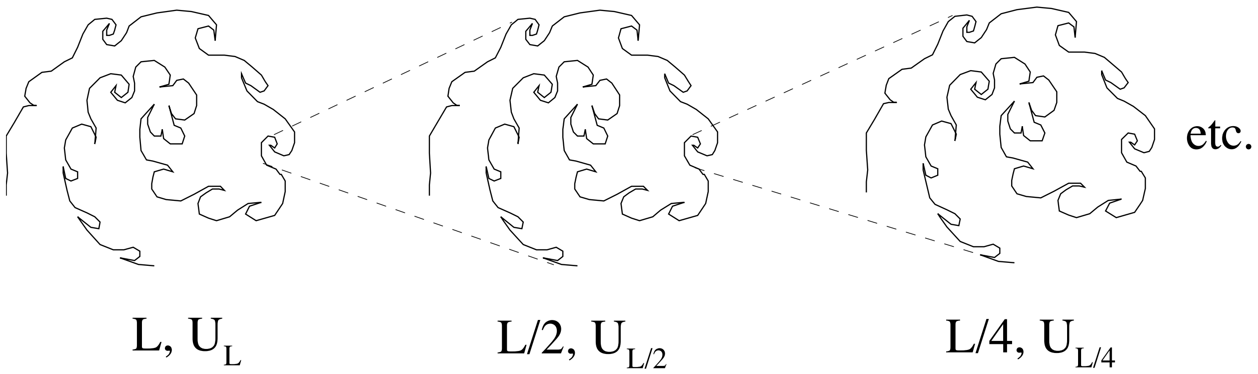

FIG. 1. – Schematic representation of the turbulent cascade. Different stages from left to right represent different magnifications of the same turbulent flow, showing eddies of decreasing characteristic lengths. The energy is transferred by instability processes towards the smaller scales, until it is dissipated by viscosity.

application is limited by the available computers to a few simple flows at low Reynolds numbers, and it is likely to remain that way for some time.

There are many good books on turbulence. The three classical ones are by Hinze (1975), Tennekes and Lumley (1972) and Townsend (1976). The first one is an encyclopaedic compilation of the experimental results available in 1959, with a mayor update for the second edition in 1975. The other two are more personal views of how turbulence should be studied, and they constitute indispensable reading for any serious student in the field. The second one, in particular, is still the best elementary introduction to the subject. The most in-depth classical treaty is the two-volume compilation by Monin and Yaglom (1975), which should be considered the last word of the classical approach, but which misses a lot of the modern developments on large scale structure. There are few comparable modern general books on turbulence. The one that best fits that description is Lesieur (1990), which is, however, biased towards the results of one particular modelling scheme. Excellent modern specialised books are by Stanišić (1988) and McComb (1990), which lean towards the formalism of the statistical description of turbulence. The second one contains enough material to be a candidate for a book of general interest. It is, for example, one of the few sources of information on the important technological field of non-Newtonian turbulence.

There are finally two books which, despite their age, remain indispensable. The short monograph by Batchelor (1953), although lacking by now in reliable experimental data, is still the reference work for the mathematical theory of isotropic turbulence, and a source of analytical ideas, many of which have not been superseded. The same applies to the book on boundary layers by Schlichting (1968) which, even if not dealing exclusively with turbulent layers, is still the best summary of their behaviour. A shorter modern book on that subject is Young (1989).

In the next two sections we review briefly the classic Kolmogorov analysis of the turbulent cascade, and the range of parameters encountered in oceanic turbulence. We next discuss briefly the question of small scale intermittency, and its importance to plankton. Finally we apply the estimates obtained in those sections to two particular problems: the possible differential concentration of planktonic particles by turbulence, and the restriction of the sensory horizon of current feeders by turbulent velocity fluctuations.

THE ENERGY CASCADE

The first fact about turbulent flows is that they are chaotic and disordered, and that they have many degrees of freedom. This, by itself, should not prevent us from computing them, since most macroscopic materials contain many more molecules than there are degrees of freedom in any turbulent flow, and statistical mechanics makes a virtue of the probabilistic aspects of these large numbers to obtain bulk properties which agree well with experiments. In turbulent flows we are also interested in mean quantities, and the fact that we cannot predict the fate of individual fluid particles is generally not important.

One of the reasons why turbulence theory is different from standard statistical mechanics is because it is dissipative. Even if viscosity has a weak effect at large Reynolds numbers, it cannot be neglected, and it influences drastically the character of the solutions. Mathematically, this is because viscosity multiplies the terms with the highest derivatives, which cannot be removed without changing the character of the equations. Physically, what happens is that it changes the number of conserved quantities. Consider the momentum equation for an incompressible viscous fluid,

$$\partial_t \boldsymbol{u} + \boldsymbol{u} \cdot \nabla \boldsymbol{u} + \nabla p = \nu \nabla^2 \boldsymbol{u} \tag{1}$$

If we multiply it by $\boldsymbol{u}$ and integrate by parts over a large volume, neglecting boundary terms, we obtain an evolution equation for the kinetic energy

$$\partial_t \int_V \tfrac{1}{2} |\boldsymbol{u}|^2 \, \mathrm{d}^3 x = -\nu \int_V |\nabla \boldsymbol{u}|^2 \mathrm{d}^3 x \tag{2}$$

It would seem that, as the viscosity ν is made smaller, the right hand side of (2) would also decrease and, in the limit of infinite Reynolds number, the kinetic energy would be conserved. That this is not so was the first experimental fact observed about turbulence, and it is the essence of the observation cited above that the pressure loss in a turbulent pipe is independent of viscosity.

The paradox was clarified by Kolmogorov (1941), who introduced the concept of an energy cascade. He imagined that turbulence is formed by "eddies" of many different sizes. Energy is injected in the largest ones, either at the boundaries or by the initial conditions, but they become unstable and transfer their energy to smaller eddies, which repeat the process to ever smaller sizes (Figure 1). As long as the eddies are large, the transfer is inviscid and no energy is dissipated, but as they become smaller in every instability, so do their Reynolds numbers. Eventually, energy reaches an eddy size (the "Kolmogorov scale") for which viscosity cannot be neglected, and the right hand side of (2) becomes appreciable. It is at this point that energy is dissipated.

The most successful prediction of this model is the form of the energy spectrum, which we will derive here as a relation between the size and intensity of the different eddies. Consider homogeneous turbulence in which the energy cascade is active at the same rate everywhere, and assume that energy is fed into the flow at some "large" scale $\ell_0 = L$ and generates eddies with characteristic velocity differences u_L. The cascade hypothesis assumes that these eddies become unstable within a time of the order of their "turnover" time $T_L = L/u_L$ and dump their energy into smaller eddies of size, say, $\ell_1 = L/2$. The rate of energy transferred per unit mass is $\varepsilon \sim u_L^2/T_L = u_L^3/L$. This process repeats itself for the smaller eddies that have just been created, and continues until the energy reaches a scale in which viscosity becomes important or, in the limit of zero viscosity, until the energy is broken into infinitesimally small eddies.

If the system is in equilibrium, the rate of energy dissipation has to be the same for all eddy sizes, and the previous argument gives the characteristic velocity u_ℓ of eddies whose size is ℓ (say between ℓ and $\ell/2$),

$$\varepsilon \approx \frac{u_\ell^3}{\ell} \quad \Rightarrow \quad u_\ell \approx (\varepsilon \ell)^{1/3}, \tag{3}$$

We can use this equation to estimate the two length scales which bound the cascade. It is customary to characterise the velocity of the largest eddies by the root mean square value of the fluctuations of one velocity component, usually along the x-axis, $u' = \left\langle (u - \bar{u})^2 \right\rangle^{1/2}$, where $\langle \, \rangle$ stands for global spatial averaging, and $\bar{u} = \langle u \rangle$. This is justified because it follows from (3) that the largest eddies contain the largest velocities. For some large eddies,

$$\varepsilon = \frac{u'^3}{L_\varepsilon}, \tag{4}$$

and this defines a large scale length L_ε, called the *integral* length, at which energy is fed into the system.

To compute the Kolmogorov scale we estimate for each eddy size the time $T_\nu = \ell^2/\nu$ which viscosity would need to damp it in the absence of turbulence. If the inviscid instability time ℓ/u_ℓ is shorter than T_ν, instabilities break the eddy before viscosity has time to act, and the latter is not important. The opposite is true if the viscous time is shorter, and the crossover happens when both are of the same order. This is the Kolmogorov dissipation length, usually called η, and given by

$$\frac{\eta^2}{\nu} = \frac{\eta}{(\varepsilon\eta)^{1/3}} \quad \Rightarrow \quad \eta = \left(\frac{\nu^3}{\varepsilon}\right)^{1/4}, \tag{5}$$

Eddies are separated in this way into two different classes. In the large ones, for which $\ell >> \eta$, instabilities act faster, and viscosity is unimportant, while the opposite is true in the small eddies for which $\ell << \eta$. The former range is called *inertial*, while the latter is called *dissipative*. In the dissipative range the flow is smooth and the velocity can be expanded as a Taylor series, with the result that the velocity differences are proportional to ℓ,

TABLE 1. – Characteristic parameters of the turbulent eddies for the different ranges of isotropic turbulence.

Range	Length	Velocity	Velocity Gradient	Decay Time
Largest eddies	L_ε	u'	$u'/L_\varepsilon = \varepsilon/u'^2$	u'^2/ε
Inertial	ℓ	$(\varepsilon\ell)^{1/3}$	$u_\ell/\ell = (\varepsilon/\ell^2)^{1/3}$	$(\ell^2/\varepsilon)^{1/3}$
Kolmogorov	$\eta = (\nu^3/\varepsilon)^{1/4}$	$u_K = (\varepsilon\nu)^{1/4}$	$\omega' = (\varepsilon/\nu)^{1/2}$	$T_K = \omega'^{-1}$
Dissipative	ℓ	$\omega'\ell$	ω'	ℓ^2/ν

$$u_\ell \approx \omega'\ell, \tag{6}$$

where the root mean square vorticity magnitude ω' has been chosen as a characteristic value for the velocity gradients.

Equating (3) and (6) at $\ell=\eta$ we can compute the order of magnitude of the characteristic velocities, gradients and time scales for the smallest eddies in the flow, which are summarised in Table 1, together with the different ranges.

It is clear from the table that the velocity and, therefore, the kinetic energy, is associated with large eddies, while velocity gradients and, therefore, the viscous dissipation $\nu|\nabla \boldsymbol{u}|^2$, are associated with eddies of the order of the Kolmogorov scale. This justifies the choice of scale for the gradients which was used in (6).

The time scale decreases monotonically with eddy size, and this has the important consequence that small eddies tend to behave as if they were in equilibrium with the local conditions imposed by the larger eddies which contain them. They evolve much faster than them, and have time to adjust their own equilibrium dynamics before the large eddies change appreciably. This is the theoretical justification for studying homogeneous turbulence as a building block for other flows, and for the equilibrium hypothesis used in (3). In most real flows turbulence is driven by large scale forces, typically shear, which differ from one situation to another. These driving mechanisms are not universal, and neither are the large scales that they produce. There is no reason to believe that the large scales of a mixing layer between two streams are similar to those of a boundary layer near a rough wall. Both are produced by different forces and look and behave differently. The hope is that, since their energy is eventually passed to smaller eddies whose sizes and lifetimes are much shorter than those of the drivers, those small scales would behave similarly in all cases, and would provide a common dissipation mechanism valid for all flows. Since these universal scales are too small to see the spatial variability of the large eddies, and too fast to sense any change in their characteristics during their own lifetime, they behave approximately as isotropic and homogeneous, and are controlled only by the local value of the energy dissipation. The theory sketched above is applicable to them.

Note next that, even if (4) and (5) are taken as definitions, they are only order of magnitudes estimates. In actual turbulence one can find some eddies which are larger than the integral scale, while viscosity may become important for eddies which are somewhat larger or smaller than η. To go beyond estimates we have to define quantitative measures of the eddy behaviour. An obvious one is the root mean square velocity difference between two points spaced by a distance , which can be used as a precise definition for the somewhat nebulous concept of characteristic eddy velocity used up to now,

$$u_\ell = \left\langle \left[u(x+\ell) - u(x) \right]^2 \right\rangle^{1/2}, \tag{7}$$

where the average is taken over $\boldsymbol{x}$, and ℓ is assumed to be parallel to the component u.

The square of this quantity is called the longitudinal second order structure function, and it follows from the previous discussion of the cascade that it should be expressible either in terms of the large scale quantities or of the Kolmogorov scales. The first representation holds only approximately, depending on the type of flow considered, but the second, which applies to the small scales near the Kolmogorov range, should be essentially universal. In the inertial range, which links both regimes, the two representations hold, and we can write

$$u_\ell = u_K F_2(\ell/\eta), \tag{8}$$

where F_2 is a universal function for $\ell << L_\varepsilon$, and tends to $F_2 = C_1(\ell/\eta)^{1/3}$ in the inertial range. C_1 is an empirical constant, $C_1=1.41$.

The main parameter characterising the small-scale velocity distribution of a particular flow is the ratio between the length scales L_ε and η, which defines the extent of the inertial range. It follows from (4) and (5) that

$$L_\varepsilon/\eta = Re_L^{3/4}, \quad \text{where} \quad Re_L = u' L_\varepsilon/\nu , \tag{9}$$

is a large scale Reynolds number. It is customary in homogeneous turbulence to write this relation in terms of a different Reynolds number, defined for historical reasons as

$$\mathbf{Re}_\lambda = (15\,\mathbf{Re_L})^{1/2} , \tag{10}$$

This *microscale* Reynolds number can be written as $\mathrm{Re}_\lambda = u'\lambda/\nu$, in terms of a length scale λ, called the Taylor microscale and intermediate between L_ε and η, but its interest is mainly historical and it is seldom used except as in (10).

Fully turbulent flows require Re_λ larger than approximately 100, and one cannot speak of real turbulence below $\mathrm{Re}_\lambda \approx 30$. The highest Reynolds numbers measured in the atmospheric boundary layer are $\mathrm{Re}_\lambda \approx 10^4$, but they are typically smaller in the ocean, due to the higher density of water with respect to air. The highest Reynolds numbers measured in tidal channels are $\mathrm{Re}_\lambda \approx 2000$, and typical values are lower, $\mathrm{Re}_\lambda \approx 200$.

A transverse structure function can be defined as in (7) for the velocity components v or w which are perpendicular to the separation ℓ. For isotropic homogeneous turbulence it can be shown (Batchelor, 1953, chapter 3) that $v_\ell^2 = w_\ell^2 = 2u_\ell^2$, and that

$$\varepsilon = \nu w'^2 = 15\,\nu\left\langle (\partial u/\partial x)^2 \right\rangle = \tfrac{15}{2}\,\nu\left\langle (\partial v/\partial x)^2 \right\rangle \tag{11}$$

It follows that the quantitative version of (6), for the velocity differences in the Kolmogorov range, is

$$u_\ell = \omega'\,\ell/\sqrt{15} \; . \tag{12}$$

The velocity distribution among eddies is often given by experimenters in terms of spectra, instead of structure functions. A full discussion of the spectral formalism is beyond the scope of this paper and can be found in any of the texts mentioned in the introduction. Briefly, the wavenumber associated to a length ℓ is $\kappa = 2\pi/\ell$, and the energy spectrum $E(\kappa)$ is defined in terms of the kinetic energy of a flow which only has eddies with wavenumbers in a certain range. Because u_ℓ contains the contribution of eddies up to size ℓ, the structure function is an integral of E, and we can estimate the spectrum from (8) as

$$E(\kappa) = u_\kappa^2 \eta F(\kappa\eta) , \tag{13}$$

were F is also universal for $\kappa L_\varepsilon \gg 1$ and tends to the classical formula $F = C_\kappa(\kappa\eta)^{-5/3}$ in the inertial range. The Kolmogorov constant C_K is related to C_1 in (8) by $C_1^2 \approx 1.3151 C_K$, and its experimental value is $C_1 \approx 1.5$ (Monin and Yaglom, 1975, 2: 351—355).

Experimental spectra and structure functions for different flows at several Reynolds numbers are shown in Figure 2. It is clear that the

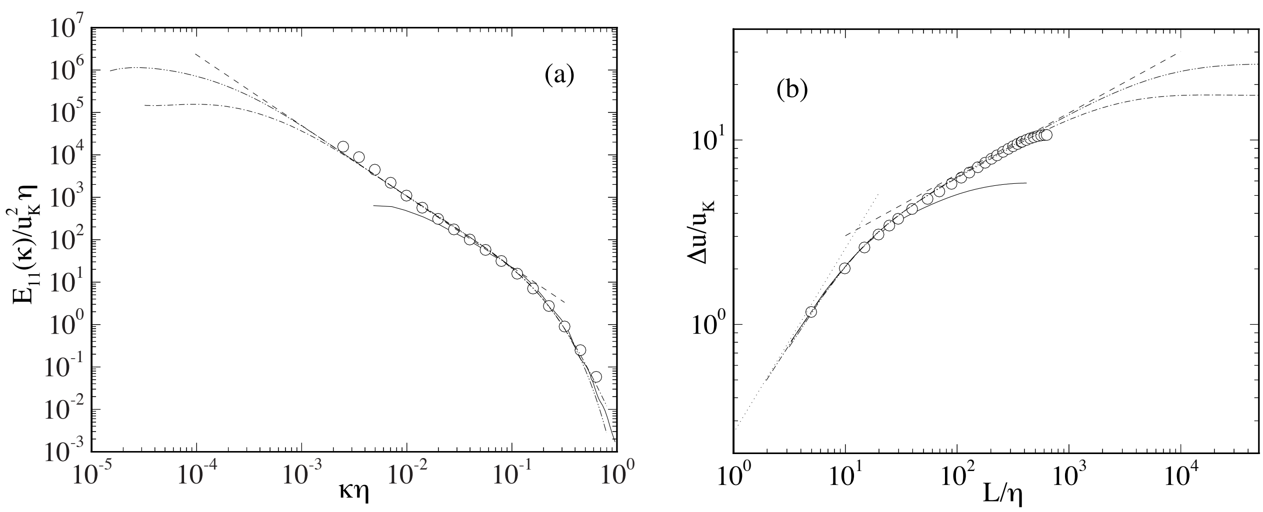

FIG. 2. – (**a**) One-dimensional spectra, (**b**) Root mean square velocity differences; both displayed in Kolmogorov scaling. Solid line: decaying grid turbulence, $Re_\lambda = 60.5$ (Comte-Bellot and Corrsin, 1971); circles: tidal channel, $Re_\lambda \approx 200$ (Grant *et al.*, 1962); Dash-dotted and dash-double-dotted: boundary layer in logarithmic region, Re_λ = 600 and 1450 (Saddoughi and Veeravali, 1994); Dashed line: inertial theory (8) and (13), with $C_K = 1.5$; Dotted line in (b): equation (12).

Kolmogorov scaling (8)-(13) works well for Reynolds numbers in a wide range. The extent of the inertial range increases with Reynolds number, in agreement with (9), and the fit to the inertial versions of (8) and (13) is good. The same is true for (12) in the dissipation range. Note however that the limit of the dissipation range in figure 2.b, at which the linear behaviour of the velocity ceases to hold, is not $\ell = \eta$, but a higher value $\ell \approx 10\eta$.

TABLE 2. – Characteristic range of parameters for small-scale, wind-driven oceanic turbulence.

u^*	$10^{-3}U_w$	1-3 cm/s
z_E	u^*/β	100-300 m
L_ε	$0.4\, z$	2-100 m
ε	$6 \times 10^{-9}\, U_w^3/z$	10^{-3}-1 cm^2/s^3
η	$100(\nu^3 z/U_w^3)^{1/4}$	0.3-2 mm
u_K	$10^{-2}(\nu U_w^3/z)^{1/4}$	0.5-3 mm/s
ω'	$8 \times 10^{-5}(U_w^3/\nu z)^{1/2}$	0.2-10 s^{-1}
Re_λ	$0.1(U_w z/\nu)^{1/2}$	200-10^4

TURBULENCE IN THE OCEAN

This is not the place to discuss the mechanisms responsible for oceanic turbulence, which is a complex and somewhat controversial subject on which excellent reviews exist (e.g. Gargett, 1989.) Our interest here is on small scale turbulence, which is supposedly independent of the production mechanism, and which should depend only on ε and Re_λ. Our only purpose is to investigate which are the typical values for those parameters in the ocean.

A useful survey is that by MacKenzie and Leggett (1993), who collected oceanic data for different situations and correlated them with the predictions of a constant-stress, wind-driven boundary layer. Their conclusion is that the theory explains a large percentage of the available data. They assume that turbulence is driven by the shear stress induced at the surface by wind, which is written by definition as

$$\tau = \rho u^{*2}, \qquad (14)$$

in terms of the water density ρ, and of a friction velocity u^*. If the wind acts long enough, the surface layer is accelerated to equilibrium, and the momentum equation requires that τ should be independent of depth. This defines a uniform scale, u^*, for the velocity, and the theory assumes that the velocity fluctuations scale with it. Experimentally, $u' \approx 2.5u^*$. The second assumption of the theory is that the integral scale at depth z is proportional to the depth, $L_\varepsilon = \kappa z$, where the Kármán constant is experimentally determined as $\kappa = 0.4$. These correlations were developed for engineering flows and have been verified for them and for the atmospheric boundary layer, although in the latter there are important corrections due to buoyancy which are also relevant in the ocean. An elementary introduction to boundary layer theory can be found in Tennekes and Lumley (1972). For wind blowing over rough (wavy) water there is an approximate empirical relation between wind

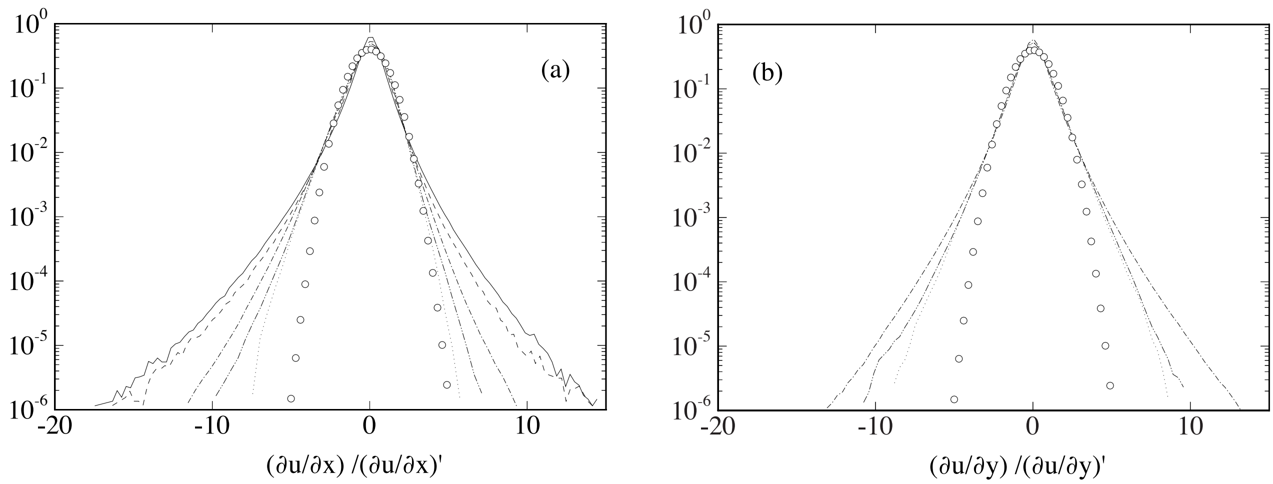

FIG. 3. – Probability density functions for (**a**) longitudinal, and (**b**) transverse velocity gradients in approximately isotropic turbulence at different Reynolds numbers. Dotted, dash-dotted and dash-double-dotted lines: Re_λ = 36, 61 and 142, direct simulation of a periodic box (Jiménez et al., 1993); dashed and solid: Re_λ = 328 and 761, stirred container in low temperature helium (Tabeling, private communication); circles: Gaussian. All p.d.f.s have been normalised to unit standard deviation.

speed as stress, which is given by MacKenzie and Leggett (1993) as $u^* \approx 1.3 \times 10^{-3} U_w$.

The constant stress layer is expected to exist for depths larger than the roughness scale introduced by the surface waves, which is a few meters, but smaller than the Eckman depth at which the Coriolis force balances the shear stress, beyond which the latter cannot be assumed to be constant. Its order of magnitude is $z_E = u^*/\beta$, where β is the Coriolis parameter. At mid-latitudes, with average winds $U_w = 10 - 30$ m/s, and $z > 5$ m, we can use these values and the discussion in the previous section to compute characteristic values for the different Kolmogorov scalings, which are summarised in table 2. Even if these are derived only for a particular driving mechanism, they seem to be representative of the values found in the ocean, above the thermocline.

INTERMITTENCY

It follows from the discussions in the previous sections that, if a small enough particle sits in a turbulent flow, it should see a velocity field varying linearly in space and randomly in time, with a typical spatial gradient of order ω', and a time scale for the variation of order ω'^{-1}. If we are interested only in distances below 10-20 times the Kolmogorov scale, the flow is essentially laminar, but time dependent. There is a tendency in physics to assume that random events are distributed according to a Gaussian distribution, in part because this is known to be true for sums of random variables under some restrictive conditions. Gaussian distributions have the advantage of being universal, in the sense that their only parameters are their means and standard deviations, and this universality is implicit in the assumption of a spatially uniform cascade used by Kolmogorov. For the velocity gradients this would mean that, since $\langle \partial u/\partial x \rangle = 0$, if we knew the dissipation in a turbulent flow, we could compute the standard deviation of the gradients, and we would know the probability of the particle finding gradients in a given range. Thus, since it follows from (11) that

$$\left\langle \left(\partial u/\partial x \right)^2 \right\rangle^{1/2} = \omega'/\sqrt{15} \ , \qquad (15)$$

we would obtain from standard statistical tables that the probability of finding a longitudinal gradient larger than ω', which corresponds to 3.8 standard deviations, would be about 10^{-4}; about 1 second every 3 hours.

It has been known for a long time that the Gaussian hypothesis is not satisfied for the increments of turbulent velocity at distances in the inertial range or shorter, and that strong gradients are more common that they would be for a Gaussian distribution (Batchelor and Townsend, 1949). This means that most of the time the gradients would still be of the order of their standard deviation, but that occasionally we should expect stronger bursts, more often than in the Gaussian case. This is the phenomenon of intermittency, which is discussed in more detail elsewhere in this volume (Jou, 1997) and which we will only treat briefly here.

As with other turbulent phenomena, intermittency is found at all scales. For the largest eddies it is associated with the non-universal large scale structures, which vary with the type of flow, but for the small eddies it is independent of the type of flow, and depends only on Re_λ. In Figure 3 we collect probability density functions for gradients at different Reynolds numbers, both longitudinal and transversal, and we compare them to the Gaussian distribution. Data for the transverse gradients are only available for the lowest Reynolds numbers, which can be computed numerically, but all indications are that the trend in the figure continues at all Re_λ; not only is their variance twice larger than for the longitudinal gradients, but their intermittency is also more marked. Their distribution is symmetric with respect to zero, while for longitudinal gradients it is not, due to the intensification of vorticity under stretching.

It should be noted that, even if it is clear from the figure that the deviations of the real probability distributions with respect to the Gaussian are substantial, they occur only at low probability levels. To continue our previous example, it can be found by integrating the probability distributions in the figure that the probability of finding a longitudinal gradient larger than ω for a flow with $Re_\lambda = 150$ would be about 3×10^{-3}, or 1 second in 5 minutes. While this is more common than in the Gaussian case, it is still a relatively rare event. Note that, from estimates in the previous section, the highest turbulent gradients are found in the shallower depths, which also have the lowest Re_λ, so that our example corresponds to the harshest conditions.

It has been found recently (Siggia, 1981; Jiménez *et al.*, 1993; Jiménez and Wray, 1994) that the reason for intermittency is the presence of strong coherent vortices, with diameters of the order of ten times the Kolmogorov scale, but with much longer lengths and probably long lifetimes. Over that small scale they contain velocity differences of the order of *u'*, both azimuthal and axial (Verzicco *et al*., 1995). They must certainly be spectacular events from the point of view of plankton, comparable to the passing of a tornado at our scale, and probably with similar consequences on the individuals involved. But they are sufficiently rare that that they can be neglected in most calculations. The curves in figure 3 fall steeply, and the probabilities decrease rapidly for the stronger gradients. If, in the previous example, we had considered a gradient ten times larger than the standard deviation, comparable in our experience to a wind gust of about 180 Km h^{-1}, the probability of exceeding it would have fallen to 6 x 10^{-6}, one second every two days.

THE EFFECT ON TRANSPORT

We move now to the application of the elementary theory to some problems of interest for the behaviour of oceanic plankton.

The intermittent vortices described in the previous section are probably important in the large scale transport of buoyant species, such as air bubbles, which get caught in the low pressure regions in the cores, and which can be transported for long times before the vortex is destroyed. Plankton and most biological materials, on the other hand, are almost neutrally buoyant, and such concentration mechanisms do not apply.

Consider first strictly neutrally buoyant particles in an incompressible fluid, and neglect forces due to rotation and lift, which are known to be small away from the strong shear found very near walls. The particles move with the fluid and can be considered as part of it. Since the fluid is incompressible, so is the particle cloud, and the concentration per unit volume does not change. Moreover, it is known that turbulence is mixing (Ottino, 1989) and that individual fluid volumes become eventually deformed and intermingled, in such a way that initial fluctuations of properties advected by the flow become homogenised after a while. Thus, even if the initial concentration of particles is not uniform, it will eventually be uniformised by the turbulence.

The characteristic time for this smoothing depends on the length scale, δ, of the initial fluctuations, and can be estimated from dimensional analysis, and from our knowledge of the important parameters in each size range. If δ is in the inertial range, the controlling quantity is the energy dissipation and the only possible combination with dimensions of time is $T=(\delta^2/\varepsilon)^{1/3}$, which can be recognised from table 1 as the characteristic eddy turnover time at size δ. This estimation of the diffusion time is equivalent to the well-known Richardson t^3 diffusion law.

For features larger than the integral scale, dissipation plays no role, since there are no eddies large enough to uniformise the concentration in one turnover. This is the range of turbulent diffusion, with a characteristic diffusion coefficient $D_E = u' L_\varepsilon$, and time scales of order $T=\delta^2/D_E$. Finally in the dissipation range, which is the one relevant to plankton, the only parameter is the mean magnitude of the gradients ω', and the homogenisation scale is the Kolmogorov time $T_K = 1/\omega'$. A good summary of turbulent diffusion, which is not however a closed subject, can be found in (Hinze, 1975).

Consider now particles with a different density than the fluid. In general they will not follow the flow, and will either lag behind or run ahead of it as it is accelerated by pressure gradients.

The equations of motion for a single particle can be simplified from the classical BBQ form (Maxey and Riley, 1983), after neglecting gravity, into

$$\frac{d\boldsymbol{q}}{dt} = -\alpha\boldsymbol{q} - \mu\frac{d\boldsymbol{u}}{dt}, \qquad (16)$$

where $\boldsymbol{u}$ and $\boldsymbol{u}_f$ are (vector) velocities of the particle and of the fluid, $\boldsymbol{q} = \boldsymbol{u} - \boldsymbol{u}_f$, and the Lagrangian derivative d/d*t* is taken along particle trajectories. The buoyancy parameter

$$\mu = \frac{\rho_p - \rho_f}{\rho_p + \rho_f/2} \qquad (17)$$

is proportional to the difference between the particle and fluid densities, ρ_p and ρ_f. For sand or air bubbles in water, $|\mu| = O(1)$, but for most biological material it is very small, $\mu \approx 10^{-2} - 10^{-3}$. If we normalise (16) in Kolmogorov quantities, the fluid velocity is $u_f \sim x$, and the damping parameter α varies between 0.1 and 10 for particles in the size range of plankton (Squires and Yamazaki, 1995). For very small particles, $\alpha \gg 1$, and the particles tend to follow the fluid. For big ones the opposite is true, and fluid and particles are decoupled for long times. The interesting range is the intermediate one, $\alpha \approx 1$, in which the particles and the fluid interact strongly, but where the particle inertia is still important.

Wang and Maxey (1993) studied the behaviour of particles in numerically simulated turbulence, in the limit in which $\rho_p \gg \rho_f$, or $\mu \approx 1$. They found that heavy particles concentrate preferentially away from the vortex cores, and reach a very non-uniform distribution. This is easy to understand, since in this limit particles are not influenced by pressure forces, and are essentially centrifuged away from the cores. They tend to travel in straight lines while the fluid rotates under the effect of pressure. This decoupling takes place in a time of the order of the eddy turnover time, which in the dissipation range is T_K, and cannot be undone by the homogenisation process mentioned above, which acts on the same time scale. Squires and Yamazaki (1995) extended the same calculation to other values of μ and found evidence of the same concentration process at $\mu \approx 10^{-2}$, in the range of biological interest. This was unlikely, for the reasons discussed next, and has since proved to be in error (Squires, pers. com.). The error was due to a subtle but common numerical pitfall, which results in an artificial concentration if the initial conditions for the particle velocities are chosen improperly. The effect is transient and the concentration is eventually homogenised.

Consider first (16) for neutral particles, $\mu = 0$. The solution can be written immediately as $q = q(0) \exp(-\alpha t)$, and the slip velocity between particles and fluid tends to zero in $t = O(\alpha^{-1})$. After that time, the particle concentration is homogenised in $t = O(1)$. The same argument is not valid for μ not zero, since the slip velocity never vanishes but, if $\mu \ll 1$ the residual velocity is at most $q = O(\mu)$, which is small, and which would take a long time, $t = O(\mu^{-1})$, to have any effect on the concentration. Since the homogenisation process acts in time $O(1)$, it is unlikely that any appreciable concentration has time to develop unless $\mu = O(1)$.

THE SENSORY HORIZON

A common model for the sensory and feeding mechanism of some zooplankton is that they generate conical currents with which they attract their prey, and whose perturbations they use as sensory input (Marrasé *et al.*, 1990). Since the individuals involved have sizes of the order of 1 mm, it follows from Table 2 and from Figure 2.b that they experience turbulence in the near dissipation range, in which the fluid velocity varies linearly with distance. We can use our knowledge of this range to estimate the distance at which the feeding currents can extend before they become weaker than the random turbulent fluctuations, and loose their effectiveness. This constitutes the effective feeding and sensory horizon of the animals, beyond which their world is masked by a turbulent "fog".

Assume an animal with a characteristic size d, which is able to generate local currents of velocity V_0. At a distance R the velocity of these currents decays as

$$V = V_0 (d/R)^2 . \qquad (18)$$

The animal is carried with the local fluid velocity, and the relative turbulent fluctuations at distance R are given by (12). Both velocities are of the same order when

$$V_0 \left(\frac{d}{R}\right)^2 \approx \frac{\omega' R}{\sqrt{15}} \quad \Rightarrow \quad \frac{R}{d} \approx 1.5 \left(\frac{V_0}{u_K} \frac{\nu}{u_K d}\right)^{1/3} . \qquad (19)$$

An important limit occurs for turbulence strong enough that $u_K^2 > V_0 \nu/d$, at which point $R < d$, and the animal becomes effectively blind, and unable to feed actively. If we assume, for example, $d = 1$ mm and $V_0 = 1$ cms^{-1}, the limiting intensity would be about $u_K = 3$ mm s^{-1}, which is within the range of strong ocean turbulent (Table 2.).

CONCLUSIONS

We have discussed briefly the basic theory of small scale turbulence as it applies to the oceanic surface layer, especially in the near dissipation range of length scales, which constitutes the immediate environment of zooplankton. We have seen that the turbulent velocity fluctuations in that range vary linearly in space, across distances which are at least an order of magnitude larger than the Kolmogorov scale. As a consequence the relevant environmental parameter for zooplankton is the root mean square turbulent velocity gradient ω'.

We have discussed briefly the effect of small scale intermittency, and shown that, while individual turbulent structures may contain gradients which are strong enough to be fatal to the animals encountering them, these encounters are so rare that they can be disregarded in lowest order calculations. The classic Kolmogorov analysis of the turbulent cascade is enough to analyse most situations of biological interest.

We have also seen that neither regular nor intermittent fluctuations are likely to cause significant differential concentration of plankton particles, of any size, unless their density differs from that of sea water by factors of $O(1)$.

We have also seen that turbulence degrades the sensory and feeding horizon of some zooplankton by interfering with the integrity of their feeding currents, and we have estimated the magnitude of the degradation. We have seen that some oceanic turbulence may be strong enough to effectively "blind" plankton in this way.

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