Turbulence and the diffusive layers around small organisms

J. R. N. Lazier* and K. H. Mann*

Abstract—We consider whether the diffusion of substances to and from a small spherical organism that is motionless relative to the surrounding water is significantly affected by the turbulent motions in the water. Viscosity, by smoothing out turbulent eddies less than a few millimeters across, dictates that the flow of nutrients and wastes to and from a very small organism must occur by molecular diffusion through a thin surrounding boundary layer. Motion of the organism relative to the water through sinking or swimming distorts this boundary layer. This alters the gradients and causes a fairly well understood increase in diffusive flux. The effect of turbulent motion on the flux, however, is less well understood. We first clarify the relationship between the size of the smallest turbulent eddies and the Kolmogorov or viscous length and go on to contend that turbulent motion over the small distances near small organisms is manifested as a linear velocity gradient whose magnitude is determined by the rate of turbulent energy dissipation. Knowing the shear enables us to calculate, from the experimental results of PURCELL (1978, *Journal of Fluid Mechanics*, **84**, 551–559), the quantitative effect of the turbulence on the diffusive flux to and from an idealized spherical organism. For motionless cells 100 μm in diameter, high levels of turbulence (dissipation rate 10^{-6} W kg^{-1}) produce a ≈2% increase in flux. This escalates to a 100% increase for cells ≈1 mm in diameter. Our results also lead to the conclusion that the microzones of increased nutrient levels surrounding small organisms, proposed by MITCHELL *et al.* (1985, *Nature*, **316**, 58–59), are much more robust than they suggested.

INTRODUCTION

RANDOM turbulent velocity fluctuations in the ocean are responsible for mixing the water and redistributing scalar properties such as heat and nutrients. The rate of mixing increases with the intensity of the turbulence, but even in the most energetic conditions found in the open ocean (dissipation ≈ 10^{-6} W kg^{-1}) the viscosity in the water smooths out fluctuations smaller than a few millimeters. Over distances less than this, turbulent fluctuations are weak and turbulent mixing is less effective than it is across greater distances. As the effectiveness of turbulent mixing declines, the transport of properties becomes more dependent on molecular diffusion. This mechanism, which is slower than turbulent diffusion over long distances, controls the flow of nutrients and wastes to and from small (≤1 mm) plants and animals which, according to SHELDON *et al.* (1972), make up more than half the total biomass of the oceans. When these small organisms require a greater supply of nutrients than molecular diffusion can deliver they are said to be "diffusion limited".

If the organisms are able to sink or swim through the water, the nutrient-depleted fluid close to the surface of the organism is replaced faster than if the organisms remained

---

* Department of Fisheries and Oceans, Bedford Institute of Oceanography, Dartmouth, N.S., Canada B2Y 4A2.

motionless. This quicker renewal increases the nutrient gradients near the cell which increases the rate of nutrient diffusion toward the cell. Munk and Riley (1952) demonstrated that differential motion increases molecular diffusion for spherical cells larger than $\simeq 20$ µm in diameter, even though the average background concentration remained constant. The authors also concluded that the effect of turbulent motions on the rate of diffusion is negligible.

In this paper we re-examine the effect of turbulence on the diffusive flux. We first demonstrate that turbulent motion across distances of 1 mm and less approximates a linear velocity gradient or shear, and then we use the experimental results of Purcell (1978), which relate the shear to the increase in the diffusive flux, to calculate the effect of turbulent motion on the diffusive flux to and from the small organisms.

To begin, we review the distributions and fluxes of substances diffusing toward and away from spherical bodies plus the effect that sinking or swimming has on the rate of molecular diffusion.

THE EFFECTS OF SWIMMING OR SINKING ON DIFFUSION

In the idealized situation of a spherical organism sitting motionless in a motionless ocean, the concentration C of a constituent diffusing outward from the surface of the organisms can be expressed (Berg and Purcell, 1977) as

$$C = (C_a - C_\infty)\frac{a}{r} + C_\infty, \tag{1}$$

where C_a and C_∞ are (respectively) the concentrations at the surface of the sphere and at a great distance from the sphere and C_∞ is assumed constant, for reasons outlined in the discussion section. The distance from the center of the sphere is measured by r, and a is the radius of the sphere. In the case of a constituent C diffusing toward the spherical organism, the equation is the same except the difference $(C_a - C_\infty)$ will be negative rather than positive. Graphs of the distributions described by this equation for inward and outward diffusion are plotted in Fig. 1 out to 10 radii from the center of the sphere at
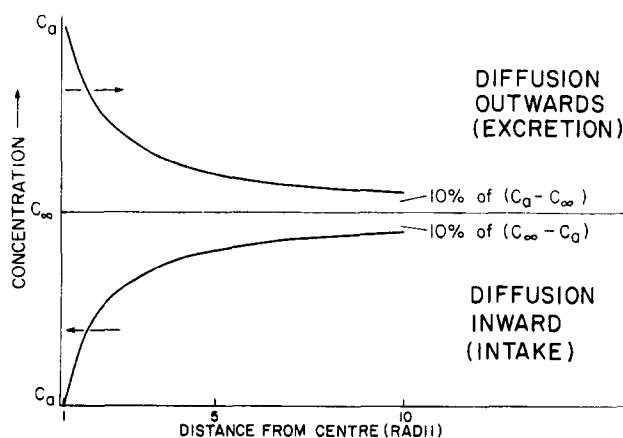

Fig. 1. Theoretical distributions, along a radius r, of materials diffusing inward and outward from a sphere of radius a calculated with equation (1). The background concentration is C_∞, the surface concentrations for both situations are C_a. The distributions are spherically symmetrical, dependent on r only.

which point the difference between C and C_∞ is 10% of $(C_a - C_\infty)$ or $(C_\infty - C_a)$. This is the assumed outer limit of the diffusive layer.

The flux of constituent C per unit area, by Fick's first law of diffusion, is

$$F = D \frac{dC}{dr},$$ (2)

where D is the coefficient of molecular diffusion, which for large molecules in water is about 2×10^{-9} m^2 s^{-1}. Taking the derivative of equation (1) and multiplying by the surface area of a sphere gives the total diffusive flux of C toward or away from the surface as,

$$F_T = 4\pi a D(C_a - C_\infty).$$ (3)

If the organism absorbs all the inwardly diffusing molecules, the surface concentration (C_a) decreases to zero and the flux, F_T, remains constant for a constant background concentration (C_∞). The organism is unable to increase its uptake of the nutrient without moving to a region with a higher background concentration or using some other strategy for increasing the diffusive flux. One strategy that can be adopted in this limiting situation is to move through the water fast enough to renew the molecules that have diffused out of the layer close to the cell at a rate faster than they can be diffused inward by molecular diffusion. Speedier renewal increases the radial concentration gradient above the value that would exist under molecular diffusion alone. The concentration gradient is then due to two processes; molecular diffusion and advection. The net result is an increase in the flux of nutrient, but it is not totally a diffusive flux.

The relative motion option was first examined by MUNK and RILEY (1952), who derived mathematical expressions for the molecular flux toward various geometric shapes as a function of velocity through the water. These expressions were derived from dimensional analyses and experimental results. We have taken their expressions for the sphere and calculated the curves shown in Fig. 2, giving the increase in the flux toward cells that are moving through the water at one and 10 diameters per second as a function of cell diameter. These curves show that relative motion of 10 diameters per second will increase the flux by a significant amount for spheres larger than 20 μm in diameter.

This problem was also addressed by BERG and PURCELL (1977). They started with the distribution of a diffusing substance described in equation (1) and combined it with the equations for the laminar flow around a sphere. Using an analytic technique they derived the curve shown in Fig. 3 which determines the increase in flux as a function of the non-dimensional variable av/D. Here a is the diameter of the sphere, v is its velocity through the water and D is the molecular diffusivity. This curve is also presented in a slightly different form in Fig. 2 for comparison with the relation derived from the work of MUNK and RILEY (1952). The curves give similar relationships except the one from the later work is displaced toward smaller sizes. It predicts that a specified increase in flux will occur for cells that are roughly 1/4 the size predicted by the curve from the work of MUNK and RILEY (1952). We do not know if this difference is significant; however, it is interesting that the two completely different analyses predict such similar results.

These results have been used successfully by various authors, including GAVIS (1976) and SOMMER (1988), in the study of nutrient uptake. The effect not so easily quantified is the one due to turbulence in the water. MUNK and RILEY (1952) considered the relative motion between the water and the organisms that turbulence would generate. This
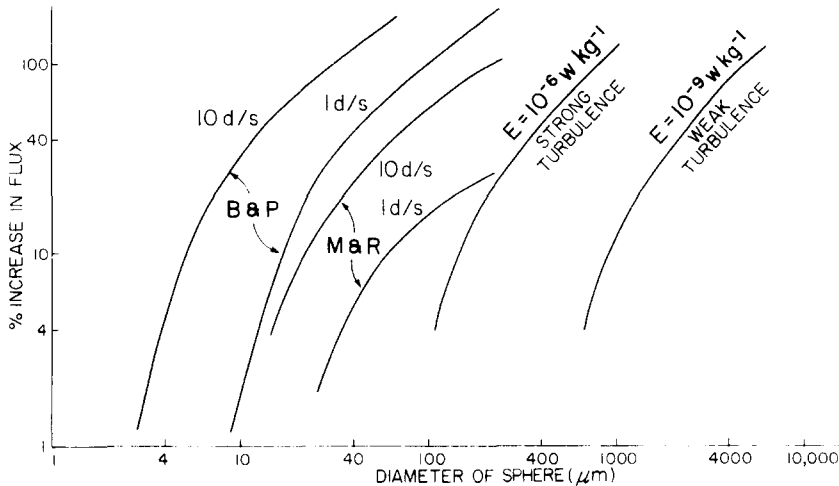
Fig. 2. Percentage increase in diffusive flux towards a perfectly absorbing sphere of diameter d caused by the relative motion of sinking or swimming at one and 10 diameters per second (d/s) and by the shear associated with turbulence. The curves for relative motion are based on the calculations of BERG and PURCELL (1977) (B&P) and MUNK and RILEY (1952) (M&R). The curves for the effect of turbulence are based on the experimental results of PURCELL (1978). The M&R curves do not extend beyond diameters of 200 μm.
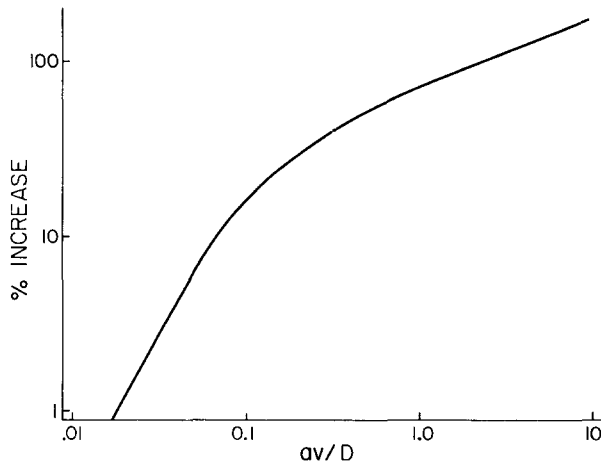

Fig. 3. Percentage increase in the diffusive flux towards a perfectly absorbing sphere due to constant laminar flow past the sphere, adapted from BERG and PURCELL (1977). The abscissa scale is a dimensionless parameter in which a is the radius of the sphere, v is the velocity through the water and D is the coefficient of molecular diffusivity.

relative motion would arise because the turbulent pressure fluctuations would cause the water to accelerate at a different rate than the organism due to the difference in density between the two. They concluded that the turbulence would have no significant effect on diffusive fluxes. We use a different approach to examine turbulent flow at small scales and show that for organisms >200 μm the turbulent motion does have a strong effect on the flux.

TURBULENCE IN THE OCEAN

Turbulent motion in the ocean originates when the well-ordered flows associated with waves, etc. break down into random fluctuations. The energy in the random motion generally appears first in eddies 1–10 m across and is then passed to smaller and smaller eddies in an energy cascade that is driven by inertial forces. As the energy is passed to smaller scales there is very little kinetic energy dissipation, but the shear increases toward the smaller scales. The higher shear causes an increase in stress due to molecular viscosity, which in turn works against the higher shears and dissipates the turbulent kinetic energy to heat. This process does not eliminate shear across small distances but it does eliminate fluctuations in the shear over small distances. The process is similar to the calming effect of oil on surface waves. The short waves are damped out by the oil while the longer waves remain unaffected, just as the small turbulent scales are damped out by viscosity while the larger turbulent eddies remain unaffected.

The size of the smallest turbulent eddies is normally discussed with reference to the Kolmogorov or viscous length, L_v. This is a length scale, devised from dimensional analysis (GILL, 1982), in which the parameters representing viscosity and the velocity shear, the two opposing factors determining the small eddy size, are combined to have units of length. The molecular viscosity is represented by v ($m^2 s^{-1}$), the kinematic viscosity or the molecular diffusivity of momentum, and the velocity gradient is represented by ε ($W kg^{-1}$), the rate of turbulent kinetic energy dissipation, and

$$L_v = (v^3/\varepsilon)^{1/4}. \tag{4}$$

v is nearly constant, $\simeq 10^{-6} m^2 s^{-1}$, and ε ranges in the ocean from 10^{-6} to $10^{-9} W kg^{-1}$ (OAKEY and ELLIOTT, 1980; OSBORN, 1978). Using this range of ε, L_v varies between $\simeq 1$ and $\simeq 6$ mm, with the smaller values being associated with the more vigorous turbulence.

The size S_s of the smallest turbulent eddies is proportional to L_v; thus,

$$S_s \simeq \alpha L_v = \alpha(v^3/\varepsilon)^{1/4}, \tag{5}$$

where α is a numerical constant which must be determined from observations.

One method of determining α is illustrated in Fig. 4, which shows some observations of shear over small scales in the mixed layer of the ocean obtained by OAKEY and ELLIOTT (1980). The data are presented, along with the theoretical universal curve due to NASMYTH (1970), in the form of an energy density spectrum defined such that the integral under the curve is equal to the total variance. The data and the theoretical curve show that the maximum energy density occurs in eddies about 40 times the size of the Kolmogorov length. Toward smaller scales the energy density decreases so rapidly that eddies five times the Kolmogorov length contain only 1% of the maximum energy. Thus these observations make it clear that there is no shear energy in the eddies the size of the Kolmogorov length, which is quite different from the impression given by GILL (1982), MITCHELL et al. (1985) and CSANADY (1986), among others, who state that the size of the smallest eddies is given by the Kolmogorov length alone. The unstated assumption of these authors is that eddies on the scale of the Kolmogorov length contain a significant proportion of the total turbulent energy.

The smallest turbulent eddies with any significant shear therefore are larger than the Kolmogorov length, but how much larger is open to question because there exits a continuum of eddy sizes with a continuous decrease in energy toward smaller sizes.
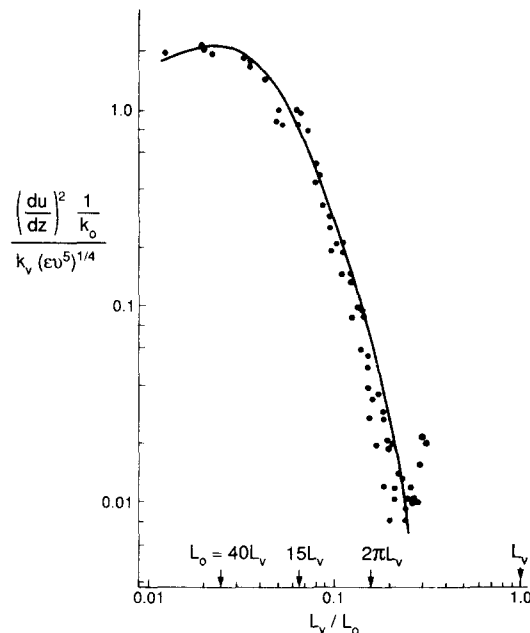
Fig. 4. A velocity shear spectra calculated from small-scale velocity measurements obtained in the mixed layer over the Scotian shelf and the theoretical curve (solid) of NASMYTH (1970), adapted from OAKEY and ELLIOTT (1980). The units of the abscissa are the ratio between the Kolmogorov or viscous length L_v and observed scales of turbulent motion L_0. The kinetic energy dissipation, ε, associated with these measurements was calculated by OAKEY and ELLIOTT (1980) to be $\simeq 10^{-7}$ W kg^{-1} which leads, via equation (4), to an $L_v \simeq 0.18$ cm. The scale of the ordinate is shear energy density scaled by the value determined from theoretical considerations.

There is no well-defined limit to the size of the eddies. PRIESTLEY (1959) discusses this situation in relation to the atmosphere and quotes the experimental results of MAC-CREADY (1953) in suggesting that $\alpha \simeq 15$. This he feels is a useful choice because 90% of the energy dissipation occurs at smaller length scales. In oceanography it is common (e.g. GARGETT et al., 1984) to define the wavenumber k_v as,

$$k_v = 2\pi/L_v = (\varepsilon/v^3)^{1/4}, \tag{6}$$

where k_v is in units of radians per meter. This usage is adopted for mathematical convenience as it reduces the appearances of 2π in the mathematical manipulations. The practice also leads to an α of 2π. From Fig. 4, eddies that are $2\pi L_v$ are seen to contain about 3% of the maximum amount of shear energy. Since the shear is proportional to the square root of the shear energy, the shear at an eddy size of $2\pi L_v$ is $\simeq (3/100)^{1/2} \simeq 1/20$ of that at $40L_v$.

The value of α is therefore a bit arbitrary, and it does not really matter what value is chosen as long as the meaning is clear. A value between 5 and 10 identifies eddies that have 1–10% of the maximum shear energy; it implies that there is no significant shear energy in smaller eddies. This is an important point when attempting to understand what goes on in the ocean at these small scales. Assuming, for example, that $\alpha = 1$ (as do MITCHELL et al., 1985) leads to an underestimate of the size of the smallest turbulent

eddies by a factor of $\simeq 10$ and a consequent overestimate of the degree of turbulent mixing at the small scales, a point we return to in the final section.

Now we wish to determine the velocity field near the microscopic organisms in the ocean, but with available instrumentation it is impossible to measure. By using the information in the spectra of Fig. 4 and the fact that water, at scales greater than molecular, is a continuous fluid, however, we have constructed the hypothetical velocity profiles (Fig. 5). The curve in Fig. 5a is an imaginary profile of velocity through 30 mm of the ocean in which turbulent eddies less than about 10 mm have been smoothed out by viscosity. The shape of this profile is both time- and position-dependent. Any other 30 mm profile will exhibit different shears on different scales, but it is unlikely to contain fluctuations that are significantly shorter than predicted by the universal spectrum of turbulent shear shown in Fig. 4. It is also generally true at small scales that turbulence is isotropic, that is, it looks much the same along all directions. Consequently the velocity profiles will be statistically similar in all directions.

Expanding a small section of this profile by 25 times might result in the profile in Fig. 5b. The velocity gradient or shear across distances of 1 mm is nearly linear because fluctuations across such small distances have been suppressed by the viscous stresses. The random nature of turbulence, however, means that the direction and intensity of the indicated shear will vary in time but over such small distances viscosity insures that the shear remains approximately linear. A further expansion of the picture by 100 times leads to the likely velocity profile surrounding a spherical organism of 1 μm radius in Fig. 5c. The shear over these small distances is more nearly linear than in Fig. 5b, but its intensity and direction still vary with time.

The organism in Fig. 5c is assumed to have the same density as water, and therefore its mass is the same as a similar sphere of water. Under this assumption the pressure fluctuations associated with the turbulence do not cause relative motion between the organism and water. This is where we diverge from MUNK and RILEY (1952), who assumed that the difference in density between the water and the organism was the only important factor in determining the effect of the turbulent motion on the molecular diffusion.

In our view the turbulent shear is a property of the fluid and does not arise from any interactions between the organism and the fluid. It is a feature of the environment
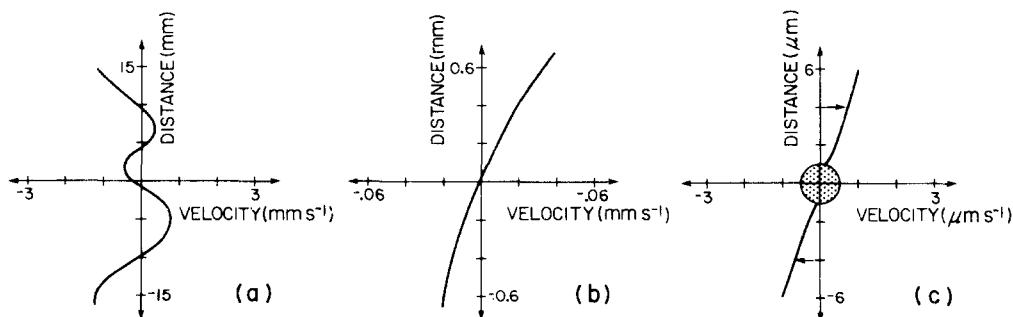

Fig. 5. (a) A hypothetical profile of velocity through 30 mm of the ocean showing the approximate size of the smaller fluctuations. (b) A magnification of the profile in (a) to illustrate the approximate constancy of the shear over scales of $\simeq 1$ mm. (c) A further magnification of the velocity profile to illustrate the velocity field close to a spherical organism of radius 1 μm.

whether the organism is there or not. Its magnitude can be estimated from the spectra in Fig. 4. For example, where the observed eddies L_0 are $\simeq 20 L_v$ the curve passes through the point where,

$$\frac{1}{k_0}\left(\frac{du}{dz}\right)^2 = k_v^2(\varepsilon v^5)^{1/4}, \tag{7}$$

which leads to,

$$\left(\frac{du}{dz}\right)^2 = \frac{\pi\varepsilon}{10v}, \tag{8}$$

when $k_v = (\varepsilon/v^3)^{1/4}$ and $k_0 = 2\pi/L_0$. If v is 10^{-6} and ε is 10^{-7} the shear is $\simeq 0.18$ s^{-1} which is about the value used in Fig. 5c.

In summary; turbulent motion in the ocean, across distances of a few millimeters, manifests itself as a linear shear. The level of the shear varies randomly with time within the range defined by the universal spectrum shown in Fig. 4, and the direction of the shear varies randomly over all directions. We now wish to examine the effect that the shear has on molecular diffusion toward or away from a small sphere.

THE EFFECT OF SHEAR ON MOLECULAR DIFFUSION TOWARDS A SPHERE

In solving the problem of determining the effect of a constant laminar flow on molecular diffusion mentioned earlier, BERG and PURCELL (1977) assumed that the organism was a perfectly absorbing sphere. Even with this simplifying assumption, determination of the effect of a linear shear flow, rather than a constant flow, is a much more difficult mathematical problem. PURCELL (1978) got around the difficulties by performing an experiment to study the corresponding problem of heat transfer from a small (9.52 mm) sphere in a sheared flow. He suspended the sphere in a liquid of high viscosity (to suppress convection) and mechanically created a shear field around it. From the temperature difference between the surface of the sphere and the fluid remote from the sphere, he was able to measure the relationship between heat flow and shear. Substituting values appropriate to molecular diffusion instead of heat transfer, his results (Fig. 6) quantified the increase in diffusive flux as a function of shear.

This result may also be recast to fit Fig. 2 by using equation (8) to convert from Ω, that is, du/dz to ε; however, we use the relation

$$\left(\frac{du}{dz}\right)^2 = \frac{\varepsilon}{7.5v}, \tag{9}$$

which is the one usually used to estimate the dissipation as a function of shear where the shear is the average value determined by integrating under the curve in Fig. 4. This relation gives a shear representative of the scales where the maximum energy dissipation is occurring (GARGETT et al., 1984), which is close to $L_v/L_0 = 0.2$ and gives a value of shear that is $\simeq 0.4$ of that derived from equation (8). This may be an underestimate for our purposes of determining a representative shear over small distances, but it does not significantly alter the end result. The results of the calculations, shown in Fig. 2, indicate that the turbulent shear causes significant enhancement of the diffusive flux for organisms of diameter greater than 100 μm, and that for an organism of a given size the diffusive flux increases with the intensity of the turbulence.
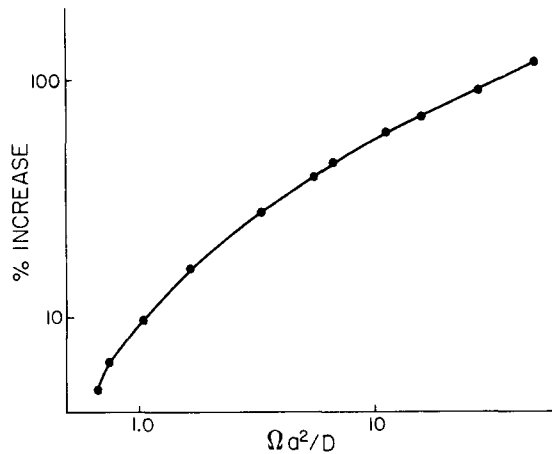
Fig. 6.   The percentage increase in the diffusive flux towards a perfectly absorbing sphere due to a shear flow, adapted from PURCELL (1978). The abscissa scale is a dimensionless parameter in which Ω represents the shear in the flow, a is the diameter of the sphere, and D is the molecular diffusivity.

DISCUSSION

The curves in Fig. 2 illustrate some simple but useful comparisons. According to the calculations of BERG and PURCELL (1977), swimming through the water at any reasonable speed has a negligible effect on the diffusive flux if the organisms are less than 5 μm in diameter, but for the larger organisms swimming will lead to rapid increase in the rate. According to the older calculations of MUNK and RILEY (1952), the effect is negligible for organisms smaller than about 20 μm, but is highly significant for organisms above this size.

If we now compare the effect of turbulence in the water on organisms that are neither swimming nor sinking, we see that the lower size limit for an effect of strong turbulence is about 100 μm, and for weak turbulence it is about 1 mm. Thus, for the larger organisms turbulence can have an appreciable effect on the diffusive flux. Figure 2 also shows that for any size of organism the effect of turbulence is small compared with the effect of swimming or sinking.

Our study also leads us to believe that the higher concentrations of excreted material in the diffusive boundary layers around small organisms are much more stable than suggested by MITCHELL et al. (1985). These authors have proposed that these regions of enhanced nutrient concentration provide more favorable conditions for bacteria than are found far from the organisms. Their calculations, however, led them to conclude that turbulent motion in the water would flush away the high concentrations, except in regions where the turbulence is weak. Our analyses indicate that for spherical organisms less than 100 μm in diameter, even the most energetic turbulence has no significant effect on the diffusion toward or away from the organism. Thus, the microzones of enhanced productivity proposed by MITCHELL et al. (1985) are probably much more robust than they thought.

We think the difference in results stems from errors in calculation. They, for example, used the Kolmogorov length scale to represent the size of the smallest turbulent eddies,

which we believe is about a factor of 10 too small. Also they grossly overestimated the thickness of the diffusion layers by substituting $C = C_\infty/10$ in equation (1) for a concentration that is above the background by one-tenth of the difference between the background and the surface value rather than $C = C_\infty + (C_a - C_\infty)/10$. Our results suggest that for organisms less than $\simeq 10$ μm the distribution of excreted material will be close to the theoretical curve for outwardly diffusing substances shown in Fig. 1. For larger organisms, sinking, swimming and possibly turbulence will increase the molecular diffusive flux by altering the concentration gradients in the boundary layer. The increase in flux means that excreted molecules stay for a shorter time in the boundary layer. This will affect the growth of smaller organisms living within the boundary layer by decreasing the size of the enriched volume and speeding up the flow of excreted molecules, but we have not attempted to estimate this effect.

One factor we ignored in our calculations using equations (1–3) is variation in the background concentration of the constituent C outside the diffusive boundary layer; that is, we assumed C_∞ to be constant. The turbulent motion of course mixes all passive scalars, but the length scale L_c of the smallest variations is not the same as L_v because the molecular diffusivity, which is one of the important factors in determining these scales, is smaller for the large molecules represented by C than for momentum. The molecular diffusivity D for the constituent C is $\simeq 2 \times 10^{-9}$ m^2 s^{-1}, whereas that for momentum, the kinematic viscosity, is about one thousand times larger at 10^{-6} m^2 s^{-1}. The scale L_c is given by BATCHELOR (1959) as,

$$L_c = (\nu D^2/\varepsilon)^{1/4}. \tag{10}$$

Using equation (4) for L_v and equation (10) for L_c, the ratio $L_v/L_c = (\nu/D)^{1/2} \simeq 20$, leading us to expect small-scale variations in the distribution of C 1/20 the size of the smallest eddies in the velocity field.

The analysis of BATCHELOR (1959) shows that the scalar C is distorted into long thin streamers by the shear in the turbulence, with the result that the gradient in C perpendicular to the shear increases until molecular diffusion is high enough to stop the gradient from increasing further. The scalar then is distributed in long thin streamers lying parallel to the flow, and on the average exhibit gradients across the shear on the spacing of L_c.

From our previous considerations we concluded that significant energy was contained in eddies larger than $10L_v$, which translates via equation (4) to sizes of 1–6 cm for dissipation rates of $10^{-6} - 10^{-9}$ W kg^{-1}. If the smaller scales in the constituent C are 1/20 of the smallest velocity scales, they will be found down to sizes of 0.05–0.3 cm.

From equation (1) the diffusive boundary layer is 10 times the radius of the sphere. For a 10 μm sphere the diffusive boundary layer is 100 μm or 0.01 cm. We therefore expect the variation in C across the shear to be 5–30 times the size of the diffusive boundary layer of a 10 μm spherical organism. The organism is therefore in an environment where the background level of C varies in both time and direction. But the length scale of the variations in C are still much larger than the organism and its diffusive envelope.

The important thing is to know how much the background varies. In the mixed layer the concentrations of all ingredients outside the diffusive boundary layers are assumed constant. In the pycnocline, on the other hand, the density gradient leads to an increase in the vertical stability of the water column and a decrease in the turbulent energy. Properties such as C also tend to vary through the pycnocline. If C represents any of the

nutrients (nitrate, silicate or phosphate) the concentrations tend to increase through the pycnocline. From the GEOSECS atlas (BAINBRIDGE, 1980), a high vertical gradient of nitrate (dNi/dz) in the mid-Atlantic upper pycnocline is $\simeq 0.1$ μM kg^{-1} m^{-1} at a mean value of $\simeq 10$ μM kg^{-1}. The maximum size of the turbulent eddies that exist in the pycnocline is about equal to the buoyancy length scale given by (GARGETT et al., 1984),

$$L_b = (\varepsilon/N^3)^{1/2}, \tag{11}$$

where N is the Brunt–Väisälä or buoyancy frequency, and ε is the turbulent energy dissipation. Again from the GEOSECS atlas, the Brunt–Väisälä frequency in the upper pycnocline is $\simeq 0.01$ s^{-1}. Thus if the turbulent energy dissipation ε is $10^{-6} \rightarrow 10^{-9}$ W kg^{-1}, L_b will vary from 1.0 to 0.03 m, respectively. And the maximum difference in the concentration of nitrate that can be expected to be generated by the turbulent motions is,

$$\Delta Ni = \frac{dNi}{dz} L_b. \tag{12}$$

Substituting $dNi/dz = 0.1$ and $L_b = 1 \rightarrow 0.03$, the maximum nitrate difference ranges from $0.1 \rightarrow 0.003$ μM kg^{-1} as the dissipation decreases from 10^{-6} to 10^{-9} W kg^{-1}. If the background values are about 10 μM kg^{-1}, the variations in the concentration of Ni over the scales of L_c will be at most a 1% fluctuation on the background value, which for this presentation is not significant.

Intermittency is another potentially important property of turbulence that we have ignored in this presentation. This is the name given to the fact that the level of turbulence is not constant or even smoothly varying through the water column but occasionally increases suddenly in patches of higher energy within a background of lower energy. These patches are caused by instabilities in the internal wave field and are similar to the occurrence of white caps when the surface waves break. We have ignored any influence of these intermittent patches by assuming that they are included in the statistical variation of the determination of the shear spectrum and the dissipation ε. Any profile along any direction, for instance, will lead to the same universal spectrum shown in Fig. 4. Each point in the spectrum is an average of a number of estimates and the average is associated with a non-zero standard deviation. The energy dissipation and the shear derived from the measurements is an average for the particular block of water that adequately serves as an estimate of the average shear around the sub-millimeter organisms even though the shear at times may be much higher or much lower than the average.

CONCLUSIONS

This investigation began as an attempt to understand how turbulence in the ocean affects the rate at which molecular diffusion transfers nutrients towards and waste products away from small organisms. Beyond not being satisfied with the available treatment of the problem we found that there is a conflict in the literature between the use of the Kolmogorov length $L_v = (v^3/\varepsilon)^{1/4}$ to represent the smallest scales of turbulent motion and the fact that the smallest observed turbulent eddies are roughly 10 times larger than L_v. We also found from talking to colleagues that turbulent flow at small scales is not well understood. A common belief is that since viscosity damps out small-scale turbulence there is no flow including shear across short distances. This by logic leads

to an ocean full of small spheres within which neither turbulent fluctuations nor shear exist because of the smoothing effect of viscosity. Then, because there is no shear within the spheres, two interior particles or organisms remain always in close proximity.

Our first goal was to clarify the meaning of the Kolmogorov length scale and its relationship to the turbulence measurements in the ocean. The fact that there is essentially no energy in the turbulent fluctuations of scale L_v was demonstrated by examination of the universal turbulent shear spectrum. It was further shown that the maximum shear in the water is found across the turbulent eddies that are ≈ 40 times the Kolmogorov length L_v, while the commonly used smallest eddy size of $2\pi L_v$, which is close to the eddy size where most of the energy dissipation occurs, exhibits a shear that is about 1/5 of the maximum.

We next used the observations of shear in the ocean in association with the idea that the shear must be continuous across even the smallest distances to demonstrate that small organisms must live permanently in a linear shear which varies randomly in direction and strength. This ubiquitous linear shear was shown, with the help of the work of PURCELL (1978), to account for a significant increase in the molecular diffusive flux toward and away from spherical organisms of 100 μm diameter and greater. However, sinking or swimming is more effective than passive exposure to turbulence in increasing the diffusive flux around organisms of all sizes.

To address the common misunderstanding of the flow at small scales we have tried throughout the paper to demonstrate that turbulent motion across small distances is simply a linear shear. The direction of the shear varies randomly in time, but the strength of the shear varies within the limits predicted by the universal spectrum. The average value of the strength increases with the intensity of the turbulence.

MITCHELL et al. (1985) drew attention to microzones of high concentrations of excretory products that surround microorganisms and which could provide optimal growth conditions for bacteria. They believed that these zones would be eroded rather easily by turbulence in the water. Our calculations lead to the opposite result. For organisms less than 100 μm in diameter, even the most energetic turbulence has no effect on the microzones, which are therefore more robust than previously suggested.

REFERENCES

BAINBRIDGE A. E. (1980) Geosecs Atlantic Expedition, Vol. 2; Sections and Profiles. U.S. Government Printing Office, Washington, D.C.

BATCHELOR G. K. (1959) Small-scale variation of convected quantities like temperature in turbulent fluid. *Journal of Fluid Mechanics*, 5, 113–133.

BERG H. C. and E. M. PURCELL (1977) Physics of chemoreception. *Biophysical Journal*, 20, 193–219.

CSANADY G. T. (1986) Mass transfer to and from small particles in the sea. *Limnology and Oceanography*, 31, 237–248.

GARGETT A. E., T. R. OSBORN and P. W. NASMYTH (1984) Local isotropy and the decay of turbulence in a stratified fluid. *Journal of Fluid Mechanics*, 144, 231–280.

GAVIS J. (1976) Munk and Riley revisited: nutrient diffusion transport and rates of phytoplankton growth. *Journal of Marine Research*, 34, 161–179.

GILL A. E. (1982) *Atmosphere–ocean dynamics*. Academic Press, New York, 662 pp.

MACCREADY P. B. (1953) Structure of atmospheric turbulence. *Journal of Meteorology*, 10, 434–449.

MITCHELL J. G., A. OKUBO and J. A. FUHRMAN (1985) Microzones surrounding phytoplankton form the basis for a stratified marine microbial ecosystem. *Nature*, 316, 58–59.

MUNK W. H. and G. A. RILEY (1952) Absorption of nutrients by aquatic plants. *Journal of Marine Research*, **11**, 215–240.

NASMYTH P. W. (1970) Oceanic turbulence. Ph.D. Thesis, Institute of Oceanography, University of British Columbia.

OAKEY N. S. and J. A. ELLIOTT (1980) Dissipation in the mixed layer near Emerald Basin. *In: Marine turbulence*, J. C. J. NIHOUL, editor, Elsevier, Amsterdam, pp. 123–133.

OSBORN T. R. (1978) Measurements of energy dissipation adjacent to an island. *Journal of Geophysical Research*, **83**, 2939–2957.

PRIESTLEY C. H. B. (1959) *Turbulent transfer in the lower atmosphere.* University of Chicago Press, 130 pp.

PURCELL E. M. (1978) The effect of fluid motions on the absorption of molecules by suspended particles. *Journal of Fluid Mechanics*, **84**, 551–559.

SHELDON R. W., A. PRAKASH and W. H. SUTCLIFFE (1972) The size distribution of particles in the ocean. *Limnology and Oceanography*, **17**, 327–340.

SOMMER U. (1988) Some size relationships in phytoflagellate motility. *Hydrobiologia*, **161**, 125–131.