

## REVIEW

# Effects of turbulence on plankton: an overview of experimental evidence and some theoretical considerations

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**ABSTRACT:** From the literature we obtained experimental data on the effects of small-scale turbulence on plankton at the organism scale. Normalized rates in response to turbulence were calculated in the present study for parameters related to growth, ingestion and energy expenditure. Growth rates are, in general, negatively affected by turbulence. Nevertheless, the data are highly biased towards a specific group of organisms, dinoflagellates, which could have peculiar physiological impediments under turbulence. Ingestion rates seem to be increased by turbulence, especially at low and intermediate levels. The few data available on energy expenditure indicate increases under turbulent conditions. Although many experiments were conducted at very high levels of turbulence with respect to oceanic conditions, in most studies the Kolmogorov size microscale remained larger than the size of the planktonic organisms. Thus, organisms responded to turbulence or turbulence-derived stimuli below the Kolmogorov lengthscale. The ecological relevance of interactions between turbulence and other size-related parameters, such as reactive distances, mean free paths and Batchelor microscales, are mentioned mainly in terms of predation, nutrient uptake and competition. Specifically, mean free paths seem relevant to determine encounter rates for organisms that show concentrations similar to those typical for large protozoa and algae (both within these organisms and between them and their potential predators). Characteristic time scales for different planktonic organisms are also explored in relation to the corresponding Kolmogorov time microscale. All planktonic organisms will experience fluctuations in the nutrient or food-particle fields over their lifetime. If other characteristic times are considered, such as the time between particle capture or nutrient uptake events, fluctuations may or may not be experienced over those times depending on the feeding mode and the turbulence intensity.

**KEY WORDS:** Turbulence · Plankton · Growth · Ingestion · Nutrient uptake · Kolmogorov microscales · Batchelor microscale · Characteristic time scales

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## INTRODUCTION

Since phytoplankton and primary production were first studied, there has been an ongoing interest in the interactions of water motion and the microorganisms living in the aquatic milieu. Large-scale turbulence can affect a range of biological processes, mostly related to the bulk distribution of cells in water. This occurs through bringing nutrient-rich water into contact with

plankton cells in the euphotic zone, creating and disturbing high density patches of organisms, and transporting plankton and detritus away from their sites of growth or production (see Thomas et al. 1997 for an overview of effects).

The possible role of turbulence as a factor inhibiting the accumulation of phytoplankton cells had an immediate application in the study of dinoflagellate blooms. Some of the dinoflagellates that form blooms also produce toxic substances that can be accumulated in shellfish and ultimately poison humans and other vertebrates. Thus, it was important to study, first, whether

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turbulence could actually prevent the growth and/or accumulation of these massive concentrations of cells and, second, the minimum levels of turbulence required to prevent this growth and the mechanisms through which this happens.

Over the last 15 yr, interest has widened to take into account direct effects of water motion, including small-scale turbulence, on individual planktonic organisms. The biological parameters studied are mainly of a physiological nature, be it in terms of growth, nutrient uptake or feeding rates on particles. These studies have resulted in a reductionist and mechanistic approach to understanding the relationships of water motion with plankton population dynamics and trophic interactions. Much of this renewed interest stems from the paper of Rothschild & Osborn (1988), who observed that fish larvae were growing successfully on concentrations of prey that were too low to result in the necessary encounter probabilities. It was argued that small-scale turbulence could add to the relative velocity between predators and prey, thus increasing encounter probabilities and, consequently, ingestion rates. Since then, the interest in small-scale turbulence has been extended to the effects on other planktonic organisms and processes.

Obtaining solid knowledge on these lines of research has been and continues to be slow because of the difficulties in tackling the problems at hand. Hard evidence of cause-effect relationships that involve water motion as a test factor is not easy to find. The reasons include a lack of firm knowledge of small-scale turbulence, one of the last frontiers in physics (Nelkin 1992), the question of comparing the intensity and quality of turbulence generated in the laboratory to oceanic turbulence (Osborn 1996), the difficulties in designing laboratory experiments under fixed, homogeneous conditions when the variable of interest is inherently random and chaotic, and others that are of a more technical nature or involve particular characteristics of the organisms being studied (Peters & Redondo 1997).

Nevertheless, sufficient research has been performed and data obtained in order to begin examining and reviewing these studies. A number of review papers on the interaction of small-scale turbulence and planktonic organisms have already been published. Most of these reviews have focused mainly on a certain group of organisms and/or are largely theoretical. The effects of fluid motion on nutrient fluxes towards and away from cells has been reviewed by Jumars et al. (1993) and Karp-Boss et al. (1996). The effects of turbulence on phytoplankton have been reviewed by Kjørboe (1993), Thomas et al. (1997), and Estrada & Berdalet (1998), while the effects on zooplankton have been reviewed by Davis et al. (1991) and Dower et al. (1997). Additionally, a few reviews have focused on the

methods of generating and measuring turbulence in laboratory or mesocosm settings (Peters & Redondo 1997, Sanford 1997, Petersen et al. 1999).

Reviews of experimental data have focused mainly on synthesizing the results and conclusions from a series of papers. There is now a critical amount of experimental data on the effects of small-scale turbulence on plankton to apply some quantitative approaches. In the present review, we compile this information across taxa and experimental setups to find general trends that can give us insight beyond that gained from individual cases. It is worth mentioning that we leave out studies of particle and colloid coagulation. Although turbulence has not often been addressed as a variable in these studies, some sort of hydrodynamic regime to generate the coagulation process is used in many of them. This has been an active field of research (see Jackson 1990, Hansen & Kjørboe 1997 or Kjørboe 1997 for some recent contributions) that deserves a separate review.

## Turbulence

The role of turbulence in the ocean and particularly how it relates to organisms has been addressed before (see Marrasé et al. 1997 for an extensive treatment on the subject).

In this section we will give a quick and very simple overview of some concepts in turbulence and oceanography as related to planktonic organisms which are necessary to understand the biological experiments that have been performed and to put these into perspective. However, the physics of turbulence is not described in detail, nor is each particular manifestation of turbulence in the ocean addressed. For further reading on these subjects see Nelkin (1994) and references therein.

Turbulent flow is an inherent property of fluid motion at high Reynolds numbers, such as those observed in the ocean. Planktonic organisms swim, take up nutrients and/or eat, grow, and reproduce in a turbulent environment, at least for part of their lifetime. Turbulent flow presents random fluctuations in velocity. Fully developed 3-dimensional turbulence is isotropic, meaning that the fluctuations do not have a preferred spatial orientation. At small scales, these fluctuations are damped out by the viscosity of the fluid. The transition between the domain where inertial forces dominate and that where viscous forces dominate is called the Kolmogorov microscale, which has length  $L_K$  (Tennekes & Lumley 1972),

$$L_K = c \left( \frac{v^3}{\varepsilon} \right)^{1/4} \quad (1)$$

where  $\nu$  is the kinematic viscosity and  $\epsilon$  is the turbulent kinetic energy dissipation rate. The leading coefficient  $c$  is usually set to unity, but empirically calculated values of order 1, or  $2\pi$  as a mathematical convenience, have also been used.

Geophysicists often refer to turbulence in the atmosphere and the upper mixed layer of the ocean as 2-dimensional or quasi 2-dimensional, because of the disparity between the largest scales of horizontal and vertical motion. In this view, universality is not guaranteed at all scales and the Kolmogorov energy cascade is not applicable (Frisch 1996). However, since we are mainly concerned with the smaller energy input scales and the small-scale turbulence derived from them, deviations from isotropy should be minor.

Sometimes the use of the term turbulence when referring to the effects on organisms smaller than  $L_K$  is of concern, since only laminar flow is present at those scales. It is true that the particle Reynolds number of most planktonic organisms is very small and hence these organisms will not experience the inertial fluctuations in velocity. However, one has to realize that at  $L_K$ , inertial and viscous forces equally dominate fluid motion.  $L_K$  is not a sharp cutoff below which no inertial motion exists. In fact, organisms considerably smaller than  $L_K$  may very well sense and/or be affected by some residual inertial motion (Hill et al. 1992). In any case a laminar shear field, scaled to  $\epsilon^{1/2}$  and derived from the smallest fluctuations or eddies, exists below  $L_K$ . The time scale  $T_K$  for the smallest eddies was also defined by

$$T_K = c \left( \frac{\nu}{\epsilon} \right)^{1/2} \quad (2)$$

and, since eddies are continuously being dissipated while others are formed, the laminar shear field at a specific point in space should also be changing in direction with the same time scale.

It is relatively easy to use theoretical equations to determine whether particles are fully or partially exposed to inertial motions, or are in a changing laminar shear field. We can then derive theoretical predictions on the effects of water motion upon those particles, in terms of distribution, encounter probability or nutrient flux towards or away from them. However, biological organisms are complex systems with complex morphologies and response behaviors, and theoretical predictions often fail to match observed data. In general, for organisms of the size of  $L_K$  or smaller, technical and methodological constraints still hinder the examination of whether an observed effect has been due to inertial motion or to the remaining laminar shear field. If we are to derive meaningful experimental results, it is crucial to correctly scale energetic conditions to those observed in the ocean.

That is, it is necessary to know whether a certain level of turbulence can increase or decrease a specific biological rate. Nevertheless, when attributing the effects of turbulence to specific hydrodynamic regimes becomes possible, we will be able to understand possible synergistic effects, generate very powerful testable hypotheses, and build mechanistic predictive models of planktonic community responses to hydrodynamics.

Hereafter when we refer to turbulence, it will be *sensu lato*. That is, as a variable affecting biological processes, it will include the more strict definition of turbulence as well as any other type of hydrodynamic motion, such as the laminar shear, derived from it. Our reasons for this decision include the fact that turbulence in the ocean is the driving force that will produce the shear fields, and that  $\epsilon$  is a convenient parameter to scale the energetic conditions in the ocean to those which organisms perceive in the laboratory.

### Biological parameters affected by turbulence

Phagotrophic planktonic organisms have to find their prey or other food particles in a 3-dimensional space. Gerritsen & Strickler (1977) developed a model for the encounter probability of prey and predator based on previous studies for naval operations (Koopman 1956). The rate at which an idealized and simplified predator would encounter prey depended on prey concentration and on the mean swimming speed of predator and prey. When encounter rates are translated into feeding rates, important energetic and behavioral consequences are derived. Rothschild & Osborn (1988) argued that oceanic small-scale turbulence has size and velocity scales similar to those of planktonic organisms (mainly zooplankton). Because of the random direction of the velocities in small-scale turbulence, this motion could increase the uncorrelated velocity between predator and prey, and in turn increase the encounter probability.

Two laboratory studies have since shown increased encounter rates between zooplankton and their prey particles owing to small-scale turbulence (Costello et al. 1990, Marrasé et al. 1990). Encounter rates were visualized with video technology. However, higher encounter rates usually did not result in higher capture rates, and the authors argued that turbulence could have disrupted the feeding currents created by the copepods. Other studies have attributed changes in parameters related to feeding under turbulence to increased encounter rates. These parameters include higher feeding rates, changes in swimming behavior that could result in higher feeding, and field correlation data between wind strength and feeding rates

(Sundby & Fossum 1990, Saiz & Alcaraz 1992b, Saiz et al. 1992, Hwang et al. 1994, Mackenzie & Kjørboe 1995). Mathematical simulations also seem to show the need for increased encounter rates owing to turbulence in order to satisfy population growth rates (MacKenzie & Leggett 1991, Werner et al. 1996). After Rothschild & Osborn (1988), further theoretical studies by these authors also conclude that encounter rate should be increased by small-scale turbulence (Osborn et al. 1991, Yamazaki et al. 1991).

It has been argued that organisms smaller than  $L_K$  should not be affected by eddy motion as the scales of fluctuation are larger than the size of the organisms. Monger & Landry (1990), in their model for direct-interception feeding of marine microflagellates, argued that neither turbulence nor Brownian motion have a significant effect upon encounter rate. They resorted to surface and hydrodynamic forces in their interception model. Lazier & Mann (1989) studied the effect of turbulence upon diffusion of substances to and from small organisms (<100  $\mu\text{m}$ ). Using previous data by Purcell (1978), they concluded that these organisms must be living permanently in linear shear fields. However, these local regions of linear velocity shear change randomly in direction and intensity, the latter increasing with kinetic energy dissipation rate. For planktonic protozoa that do not create feeding currents, Shimeta & Jumars (1991) and Shimeta (1993) hypothesized that laminar shear fields could significantly increase encounter rates with prey particles. Shimeta et al. (1995) experimentally investigated the effect of a laminar shear field on the ingestion rate of different protozoa, including ciliates, flagellates and heliozoa. Their results seemed to depend on the feeding and swimming behavior of the different protozoa, and show the strongest effects of turbulence on feeding for non-motile protozoa. However, while positive results imply that higher ingestion rates are caused by a higher encounter probability, lower ingestion rates or no effect does not necessarily mean lower or unaffected encounter probability, since the physiology and behavior of the organisms can strongly interact with the physics of the process, causing particles that are encountered to be rejected.

If we are to resolve the encounter rate problem at the micrometer scale, we need to be able to track the movement of particles in 3 dimensions under a range of hydrodynamic conditions and to visualize actual feeding processes. However, this is not possible with the video technology currently available; therefore the presence or absence of laminar shear fields and eddy motion at these scales remains theoretical, and so encounter rates will have to continue being assumed theoretically or inferred from processes tainted with biological variability.

## MATERIAL AND METHODS

**Data collection.** From the literature we obtained experimental papers that included turbulence or some other parameter related to water motion as an experimental factor affecting planktonic organisms. To find these papers, we searched the 'Current Contents' database for the keywords 'turbulence', 'shear' and 'hydrodynamic' and their derivatives. Additionally, we explicitly searched many journals that have published papers on experiments with turbulence and plankton, including Limnology and Oceanography, Marine Ecology Progress Series, Journal of Plankton Research, Deep-Sea Research, and ca 50 more. Finally, we also looked into the reference lists of review papers. Specifically, we compiled data on the biological variable tested under both turbulence and a still water reference or control, the level of turbulence, size and swimming velocity of the organisms tested, and the temperature at which the experiment was conducted. Not all parameters were available all the time in the source papers. In some cases we could fill in gaps with literature information such as on the sizes of organisms, or apply equations such as for swimming velocities of phytoplankton based on their sizes (Sommer 1988).

**Conversion to  $\epsilon$ .** The papers had to have a quantification of the turbulence intensity assessed, or have enough information to make an approximate calculation based on theoretical assumptions. We chose to standardize the quantification of turbulence based on the turbulent kinetic energy dissipation rate ( $\epsilon$  with units of  $\text{cm}^2 \text{s}^{-3}$ ).

When shear ( $\gamma$ ;  $\text{s}^{-1}$ ) levels were the only quantifiable parameter in the source paper, we calculated  $\epsilon$  based on the expression  $\gamma = c(\epsilon/\nu)^{1/2}$ . The constant  $c$  was set to unity unless the authors explicitly referred to a different value in the paper. In most of these cases the authors used Couette cylinders to assess the effect of laminar shear on the organisms. However, the laminar shear that the organisms are hypothesized to experience derives from the breakdown of the smallest eddies. In that sense, we calculated the  $\epsilon$  that would be needed to produce the reported level of shear.

In some papers, especially in the early literature, researchers used flasks on shaker tables, and turbulence was rarely quantified. When information on the geometry and dimensions of flasks, and their incubation volume, as well as on the frequency of oscillation and the diameter of the orbit was provided in the source, we estimated energy dissipation rate as follows:

$$\epsilon = (O) \cdot \frac{u^3}{L} \quad (3)$$

where (O) means 'of the order',  $u$  is a characteristic velocity calculated as  $d \cdot f$  ( $d$  being the distance trav-

eled in one oscillation and  $f$  the frequency of oscillation in Hz), and  $L$  is a characteristic lengthscale. We derived  $L$  from a volume to surface ratio ( $V/S$ ) where  $S$  is the surface in contact with the fluid and can be derived from the reported flask geometry.

In other cases turbulence was generated with oscillating grids. Again, when no quantification of turbulence was given in the source paper but we had information on the grid and container dimensions and on the oscillation frequency and stroke length, we estimated  $\varepsilon$  assuming that all the kinetic energy produced by the grid goes into turbulent motion. There is a good agreement between these theoretically calculated values and those measured experimentally (Peters & Gross 1994, Saiz 1994). From the grid dimensions we calculated the solid area of the grid ( $GSA$ ), and from the oscillation frequency and stroke we obtained  $u(t)$ , the vertical velocity of the grid. Then we applied the following expression (Peters & Gross 1994):

$$\bar{\varepsilon} = \left( \frac{1}{T/4} \right) \int_0^{T/4} \frac{C_d GSA}{V} u(t)^3 dt \quad (4)$$

where  $T$  is the period of oscillation,  $C_d$  is the drag coefficient for the grid, and  $V$  is the volume of the fluid in the container. We used a constant  $C_d$  of 0.7. This value was chosen arbitrarily based on our experience with free falling grids in the laboratory (data not shown). Strictly,  $C_d$  depends on the grid Reynolds number ( $Re$ ), which is continuously changing in an oscillation cycle from 0 to  $Re_{max}$ , and  $Re_{max}$  depends on the oscillation frequency and stroke. There are empirical relationships of  $C_d$  versus  $Re$  for particular shaped and sized grids in the literature, but their application is not straightforward to other grids and tends to be restricted to certain domains of  $Re$ , say for  $Re \ll 1$  or for  $Re > 1000$ . When we compared calculations of  $\varepsilon$  based on constant or changing grid  $C_d$ , the values were within 1 order of magnitude. Thus, we preferred to use the constant  $C_d$  rather than an equation that might be in error.

In all our calculations we used a  $\nu$  of  $0.01 \text{ cm}^2 \text{ s}^{-1}$ , a value typical of 35 psu water at  $22^\circ\text{C}$ . Salinity information was rarely given in the source papers and the range of temperatures extended from  $7$  to  $28^\circ\text{C}$  with an average of  $17 \pm 4^\circ\text{C}$ . Assuming seawater of 35 psu, an average  $\nu$  of  $0.0112 \text{ cm}^2 \text{ s}^{-1}$  would be obtained (Jumars et al. 1993), which is relatively close to the  $0.01 \text{ cm}^2 \text{ s}^{-1}$  used. In any case, the error introduced should be small compared to errors made by other assumptions, and even by direct measurements.

**Conversion to a normalized parameter.** The parameters that were tracked ranged from cell numbers or chlorophyll concentrations to ingestion rates. To compare the effects of turbulence on these parameters across experiments, organisms, and other varying con-

ditions we normalized the measured rates with the following formula, provided a still water control was available:

$$rate_x = \frac{rate_{tur} - rate_{control}}{|rate_{control}|} \quad (5)$$

where  $rate_x$  is the normalized rate and  $rate_{tur}$  and  $rate_{control}$  are the rates under turbulence and still water control conditions, respectively. When  $rate_x$  is positive, turbulence had an effect increasing that rate above that of the control condition, and when  $rate_x$  is negative, turbulence decreased the rate to levels below that of the control. At  $rate_x = 0$  there is no effect of turbulence on the measured rate. There is one case in which  $rate_x$  cannot be calculated, namely when  $rate_{control} = 0$ , Eq. (5) is not defined. Fortunately, this happens rarely.

In order to extract generalities from the information of the parameters measured, we divided them into 3 categories. In the first category we fitted all those parameters which had a relation to ingestion rate of particles, and in the second one, those parameters related to organism growth. Finally, the third category covered parameters related to energy expenditure, such as respiration measurements.

## RESULTS AND DISCUSSION

We found 38 sources that contained experimental results of planktonic organisms subjected to turbulence. Out of these, 26 (totaling 452 data points) contained enough information to calculate rate parameters, both under turbulence and still water control conditions (Table 1). One data point had to be eliminated because  $rate_{control} = 0$  (see 'Materials and methods'). Organisms ranged from bacteria to fish larvae, covering 4 orders of magnitude in size.

The data of  $rate_x$  were not normally distributed for any of the 3 categories (Kolmogorov-Smirnov test). For a summary of descriptive statistics see Table 2. Of course values of  $rate_x$  around 0 could be real effects of turbulence (positive or negative) or could just be experimental variance. Since the nature of the data prevented the calculation of confidence intervals, we chose a value of  $|rate_x| = 0.5$  as the cutoff to consider an effect of turbulence. That is, there should be at least a 50% increase or decrease of the rate under turbulence with respect to the still water control to be considered as an effect owing to turbulence, and not attribute the difference to error. We checked this assumption by randomly picking a subset of data for which the original sources had performed some statistical analysis or we could calculate a statistic with the given information, and compared the results with  $rate_x$ . In 83% of the cases our cutoff matched the statistical analysis, and



Table 1. Data sources on the effects of turbulence on planktonic organisms and some of their characteristics (LDV: laser Doppler velocimetry; ADV: acoustic Doppler velocimetry)

Organism	Turbulence generation	Turbulence measurement $\epsilon$ ( $\text{cm}^2 \text{s}^{-3}$ )	Variable	No. of data points	Source
<i>Gonyaulax excavata</i>	Rotary shaking	Estimated (Eq. 3) <sup>a</sup> : 43–119	Growth	5	White (1976)
<i>Peridinium cinctum</i>	Rotary shaking	Estimated (Eq. 3) <sup>a</sup> : 43	Nuclear division	1	Pollinger & Zemel (1981)
<i>Phaeodactylum tricornutum</i> , <i>Brachiomonas submarina</i>	Oscillating grid	Estimated (Eq. 4) <sup>a</sup> : 2.3–2300	Growth	8	Savidge (1981)
<i>Centropages hamatus</i>	Vibration	Particle velocities (cinematography): 0.05–0.15	Encounter	2	Marrasé et al. (1990)
<i>Gonyaulax polyedra</i>	Couette cylinder	Estimated: 0.045–164	Growth	10	Thomas & Gibson (1990a)
<i>Gonyaulax polyedra</i>	Couette cylinder	Estimated: 0.045–164	Growth	10	Thomas & Gibson (1990b)
<i>Proocentrum micans</i>	Orbital shaker	Estimated (Eq. 3) <sup>a</sup> : 11–16	Growth	2	Berdalet (1991)
<i>Zoogloea ramigera</i> , <i>Escherichia coli</i>	Shaker table	Estimated: 400	Uptake	6	Confer & Logan (1991)
<i>Acartia</i>	Oscillating grid	Estimated (Eq. 4) <sup>a</sup> : 12.5	Growth efficiency	12	Saiz & Alcaraz (1991)
<i>Gymnodinium nelsonii</i>	Orbital shaker and oscillating grid	Estimated (Eq. 3) <sup>a</sup> : 20	Growth, RNA/DNA	1	Berdalet (1992)
<i>Tetrahymena</i>	Gyratory shaking	Estimated (Eq. 3) <sup>a</sup> : 117–216	Growth	5	Hellung-Larsen & Lyhne (1992)
<i>Acartia</i>	Vibrating grid	Particle velocities (cinematography): 0.01–0.05	Feeding behavior	13	Saiz & Alcaraz (1992a)
<i>Acartia</i>	Reciprocal shaker	Estimated (Eq. 3) <sup>a</sup> : 0.009–0.052	Excretion	3	Saiz & Alcaraz (1992b)
<i>Acartia</i>	Oscillating grid	Estimated (Eq. 4) <sup>a</sup> : 0.17–1.86	Feeding	55	Saiz et al. (1992), Saiz (1991)
<i>Gymnodinium sanguineum</i>	Couette cylinder	Estimated: 0.011–18	Growth	10	Thomas & Gibson (1992)
<i>Dunaliella viridis</i>	Air bubbling	Estimated: 6.8–480	Growth	5	Aguilera et al. (1994)
Crustaceans	Vibrating grid	Estimated: 0.05	Heartbeat	25	Alcaraz et al. (1994)
Microplankton and <i>Paraphysomonas imperforata</i>	Oscillating grid	Particle velocities (LDV): 14.5	Grazing, feeding	2	Peters & Gross (1994)
<i>Acartia tonsa</i>	Oscillating grid	Particle velocities (LDV): 0.1	Feeding	10	Saiz (1994)
<i>Gadus morhua</i> , <i>Clupea harengus</i>	Oscillating grid	Particle velocities (ADV): 0.00074	Feeding	17	MacKenzie & Kiørboe (1995)
Purple sea urchin gametes	Couette cylinder	Estimated: 27–16000	Fertilization	10	Mead & Denny (1995)
Bacteria	Shaker table	Estimated: 210–420	Growth	15	Moeseneder & Herndl (1995)
<i>Acartia</i>	Oscillating grid	Particle velocities (cinematography): 0.004–3.7	Feeding	120	Saiz & Kiørboe (1995)
Nine different protozoa	Couette cylinder	Estimated: 0.008–43	Feeding	71	Shimeta et al. (1995)
<i>Gonyaulax polyedra</i>	Couette cylinder	Estimated: 0.071–7.71	Growth, efficiency	22	Thomas et al. (1995)
<i>Paraphysomonas imperforata</i>	Oscillating grid	Particle velocities with LDV: 0.05–5	Growth, feeding, efficiency	12	Peters et al. (1996)

<sup>a</sup>Estimation done in this study from information in the source papers

when not, it was cases such as a  $rate_x$  of 0.57 being not significant or a  $rate_x$  of  $-0.48$  being significant, i.e., values very close to the cutoff of  $\pm 0.5$ .

Table 2. Summary of descriptive statistics for the different  $rate_x$

	Growth	Ingestion	Energy expenditure
N	139	268	44
Min.	-2.92	-1.00	-0.40
Max.	4.26	6.03	1.24
Mean	-0.21	0.32	0.26
Variance	0.76	0.88	0.10
Skewness	0.90	2.84	1.16
Kurtosis	8.01	11.40	1.39
Median	-0.11	0.10	0.15

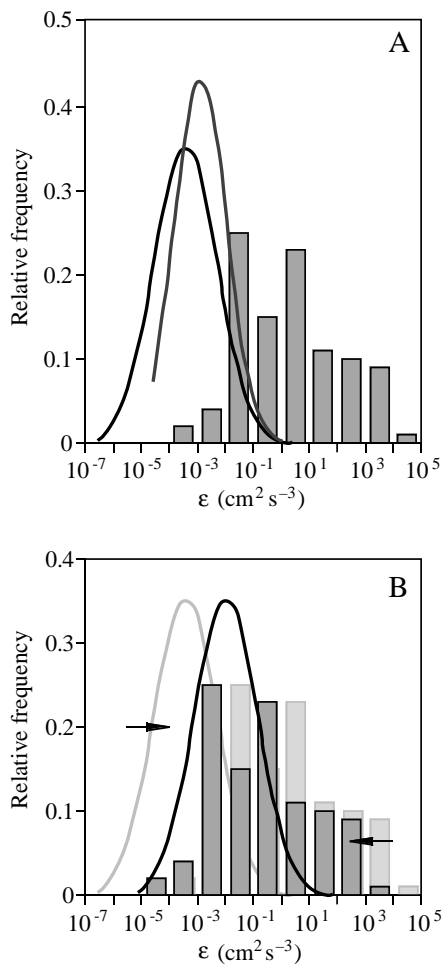


Fig. 1. Comparison of turbulence levels used in studies with plankton (bars) with turbulence levels compiled from the ocean (MacKenzie & Leggett 1993) (lines). Redrawn after Peters & Redondo (1997). (A) Lines generated from all turbulence data (continuous line) and from non-wind generated turbulence (broken line) in MacKenzie & Leggett (1993). (B) Speculative convergence of the 2 datasets (see 'Turbulence intensities')

## Turbulence intensities

The turbulence intensities in the dataset ranged from  $7.4 \times 10^{-4}$  to  $1.5 \times 10^4$   $\text{cm}^2 \text{s}^{-3}$  with a geometric mean of 0.98. Values reported for the ocean range from  $2.8 \times 10^{-7}$  to  $47$   $\text{cm}^2 \text{s}^{-3}$  (Osborn 1980, MacKenzie & Leggett 1993, Simpson et al. 1996, Terray et al. 1996). Thus, while many of the laboratory-generated turbulence levels are realistic of oceanic conditions, or at least can be found in the ocean at certain locations or under certain circumstances, the distribution of turbulence intensities that have been reported in laboratory studies is, on average, higher than average values of turbulence reported for oceanic conditions (Fig. 1A). This is of concern when extrapolating laboratory results to the natural environment.

However, there are reasons to believe that this large difference is artificial. First, it is not easy to simulate low turbulent energy dissipation rates in the laboratory. Energy input scales are much smaller than under natural conditions, thus narrowing the inertial sub-range, while still a significant amount of energy has to be introduced in order to create turbulent flow at all. As a consequence, the equations applied to calculate turbulence may sometimes violate the assumption of having a fully developed inertial sub-range and perhaps give incorrect values (Osborn 1996). Second, field measurements have mostly been carried out under relatively calm conditions, a purely logistical constraint, biasing average oceanic turbulence levels to the lower end (Peters & Redondo 1997). Third, most oceanic measurements have been performed in deep waters and below the upper tens of meters because of constraints with measuring probes. As more data are being gathered, especially from the upper meters of the surface mixed layer with newer microstructure profilers (Anis & Moum 1995, Moum et al. 1995) and from tidally mixed seas (Simpson et al. 1996), it appears that turbulence levels can be several orders of magnitude higher than previously reported. It is worth noting that the bulk of the planktonic activity in the ocean takes place in the upper meters of the ocean and in coastal systems, precisely where turbulence measurements seem to have been underestimated.

In summary, we really do not know how biased turbulence levels used in biological experiments may be with respect to oceanic conditions or to the environments where most of the planktonic activity occurs. From the above considerations, it may turn out that the intensities are very similar and we may speculate on a closer match between the experiments and natural conditions (Fig. 1B). Additionally, the Kolmogorov microscales derived from the turbulence intensities (Fig. 2) do not show such large differences between turbulence in the ocean and in the laboratory, because

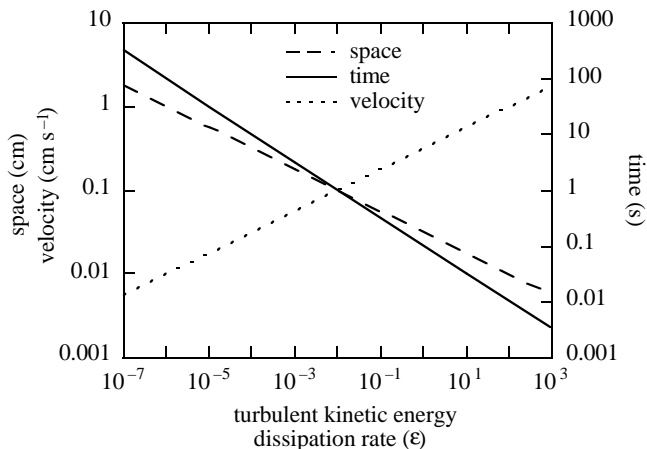


Fig. 2. Calculated Kolmogorov microscales against turbulence intensity. Kinematic viscosity:  $0.01 \text{ cm}^2 \text{ s}^{-1}$

their calculation includes fractional powers. For instance, a 100-fold difference in  $\epsilon$  turns out to be only a 3.3-fold difference in  $L_K$ .

Perhaps a more difficult aspect to address will be to reconcile the inherently large spatial and temporal variability of shear, and consequently turbulence, in the ocean (Gargett 1997) with the need to test the effects of defined and constant levels of turbulence upon organisms and rate processes to establish firm cause-effect relationships.

### Growth rates

Turbulence on average shows a negative effect on growth rate (higher growth rates under still water conditions) (Fig. 3A). However, the data are highly influenced by the results from dinoflagellate studies. The results from the dinoflagellates all belong to the 20 to 200  $\mu\text{m}$  size class, and as a group they show the strongest and most unequivocal response to turbulence ( $\text{rate}_x = -0.91 - 0.31\log(\epsilon)$ ;  $R = 0.55$ ), with a bulk 121% decrease in the normalized growth rate. When the dinoflagellate data are taken out, this trend is reversed (Fig. 3B) and the cloud of growth rates is now slightly positive under turbulence, although since the difference is small we cannot distinguish it from 0. The largest positive effects are seen for organisms larger than 200  $\mu\text{m}$ , mainly calanoid copepods.

Dinoflagellates could be physiologically impeded under turbulence. Berdalet (1992), found that *Gymnodinium nelsonii* stopped dividing under turbulence, while at the same time increased in size. The author argued that turbulence could alter some cytological aspect of the cells. Since in many unicellular organisms the basal bodies of flagella are identical to the centrioles necessary for nuclear division (Margulis et al.

1990), there could be a relation between an impediment in swimming and an altered division process in a turbulent field.

Most of the data for dinoflagellate growth under turbulence assessed the effect of turbulence-derived shear (using Couette cylinders) on one dinoflagellate species. Hence, the chances that the response to turbulence is particular to that species under that laboratory setup are high. Obviously, more data are needed with a range of species, both dinoflagellates and other phytoplankton, to know whether such responses can be generalized to all dinoflagellates or even to all phytoplankton, or just to certain taxa or organisms that have certain characteristics, e.g., the ability to swim.

Couette cylinders are designed with constrained dimensions to generate a constant shear stress when operated under a specific set of parameters. As is also the case with other setups, subjecting the organisms to constant conditions for long periods of time with respect to their inherent time scales may introduce other sources of variability. Certainly, these long constant hydrodynamic regimes are not characteristic of

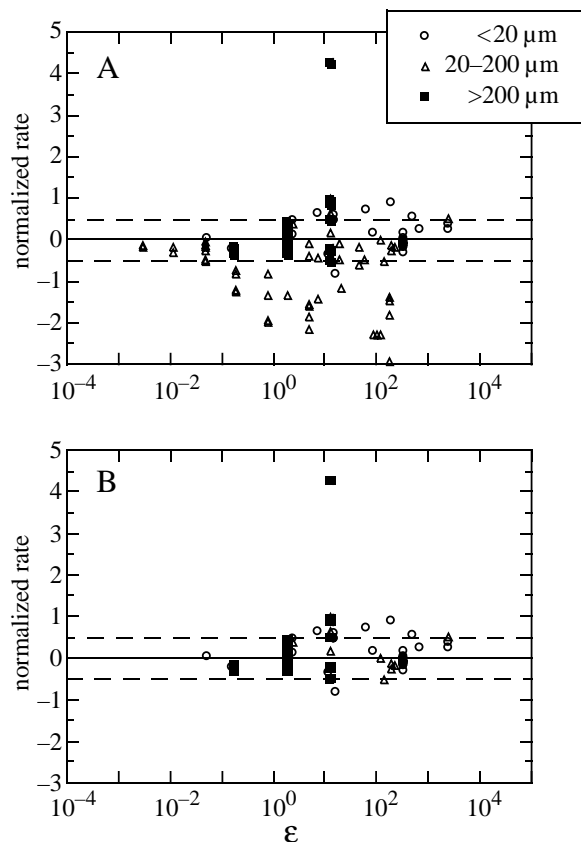


Fig. 3. Normalized rate for growth related parameters against turbulence intensity, in experiments with plankton. Symbols denote different plankton size classes. Broken lines show the  $\pm 0.5$  cutoff. (A) All data; (B) without dinoflagellate data



field conditions. For instance, organisms could adapt their physiology to the hydrodynamic condition encountered. Perhaps dinoflagellates encyst or enter some other type of resting stage. But, on the other hand, the flow in a Couette cylinder can easily become unstable (Tritton 1988) and just introducing a pipette to take a sample may produce instabilities that propagate in time. So, after all, some of these organisms occasionally may have been subjected to other hydrodynamic conditions. Gibson & Thomas (1995) found that 5 to 15  $\text{min d}^{-1}$  of shear above a certain threshold would be sufficient to introduce a negative effect on growth. Thus, it would seem that there really is a direct effect on growth. As more data are gradually becoming available (Hondzo et al. 1998), this slower growth under turbulence seems to be more generalized at least at high intensities, and we may soon be in a position to generalize this outcome.

### Ingestion rates

For phagotrophic organisms, ingestion rates and/or encounter rates (Fig. 4) seem to be favored at all but the highest levels of turbulence. Although negative effects (lower ingestion rates) of turbulence are reported at all  $\epsilon$  levels studied and for the whole range of organism sizes, positive effects dominate the dataset especially below levels of  $10 \text{ cm}^2 \text{ s}^{-3}$ . Although all size classes present positive averages, only the 20 to 200  $\mu\text{m}$  class shows a marked effect under turbulence (110% higher ingestion rates). All the organisms in this size class are protozoa and the results come from a single study (Shimeta et al. 1995). Several protozoa from different groups were tested but, again, more data will be needed before generalizations can be made. The  $<20 \mu\text{m}$  size class shows only minor positive effects at

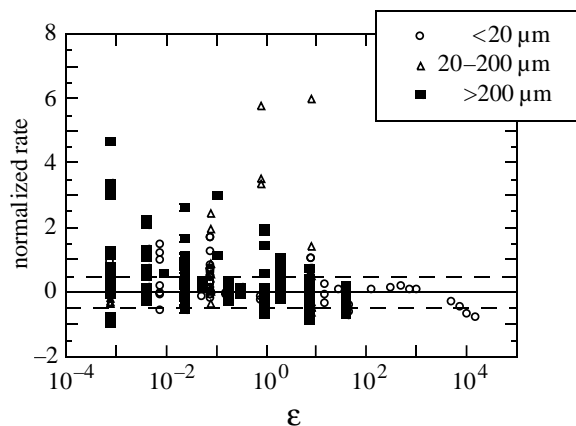


Fig. 4. Normalized rate for ingestion related parameters against turbulence intensity, in experiments with plankton

intermediate levels of turbulence, and high turbulence levels do not increase ingestion. In the  $>200 \mu\text{m}$  size class there is a clear tendency for positive effects to decrease with increasing turbulence.

Several studies have shown that the theoretically predicted (Rothschild & Osborn 1988) and experimentally observed (Marrasé et al. 1990) increases in encounter probability between copepods and their prey owing to turbulence do not always result in higher ingestion rates (Saiz 1994, Saiz & Kiørboe 1995, Caparroy et al. 1998). MacKenzie & Kiørboe (1995) reached the same conclusion for larval fish. These studies and others of a more theoretical nature (MacKenzie et al. 1994, Jenkinson 1995, Kiørboe & MacKenzie 1995, Kiørboe & Saiz 1995) found that the influence of turbulence on ingestion rates depends not only on the increase in encounter rates but also on many biological-related aspects like predator swimming and searching mode and behaviour, prey type and effects on the reactive distance. A dome-shaped relationship of ingestion versus turbulence was found in some cases. Briefly, low turbulence levels have insignificant effects on ingestion rates, intermediate levels show increases in ingestion and high levels again have insignificant or even negative effects on ingestion since they would interfere with prey capture by eroding the feeding currents or reducing reactive distances.

Protozoa also show a variety of searching and behavioral patterns and many use some type of feeding current to capture prey particles. Thus, ingestion for some protozoa might also show the dome-shaped response to turbulence through processes similar to those described for copepods and fish larvae, although inertial forces should be damped out at their size scale and the physical forcing would probably be shear.

### Energy expenditure rates

As mentioned in the 'Material and methods' section, a few observations were related to metabolic activity, such as respiration, excretion, etc., and were standardized to energy expenditure. The few data points in this dataset, especially for organisms smaller than 200  $\mu\text{m}$ , make it difficult to discern differences. If anything, organisms tend to increase their energy expenditure under turbulence (Fig. 5). Alcaraz et al. (1994) suggested that the response of calanoid copepods to turbulence is analogous to the response to an increase in temperature. This implies an increased activity and a decrease in energetic efficiency. The common thread would be that in both cases there would be an increase in entropy, related to temperature at the molecular level in one case and to velocity fluctuations at the scale of the organism in the other.

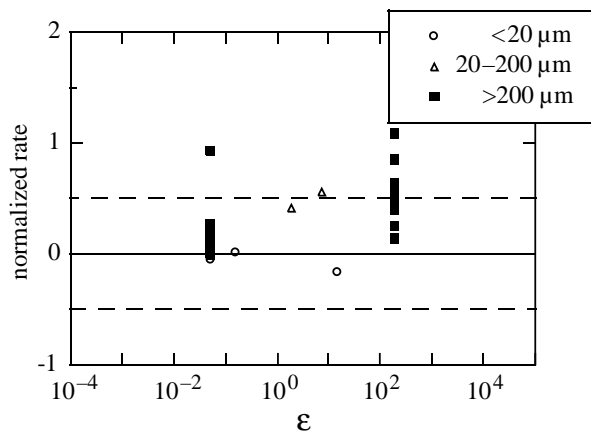


Fig. 5. Normalized rate for parameters related to energy expenditure against turbulence intensity, in experiments with plankton

### Balancing the budget

Growth is related to ingestion of particles or uptake of dissolved substances through a conversion efficiency, and the relationship can be stated as:

$$GR \propto IR \cdot CE \quad (6)$$

where  $GR$  and  $IR$  are the specific rates of growth and ingestion or uptake respectively and  $CE$  is a conversion efficiency. The energy expenditure rates calculated in the present study can be considered a surrogate for the inverse of  $CE$ . The values for the different terms are not constant but may change depending on different internal and environmental conditions. For instance,  $IR$  can change depending on food concentration under non-saturating conditions. All 3 terms have been shown to vary, at least sometimes, when organisms are subjected to turbulent conditions.

Referring this relationship to the  $>200 \mu\text{m}$  size fraction data it seems that  $IR$  has a tendency to increase, while  $CE$  has a tendency to decrease, and  $GR$  does not seem to vary. These data come from experiments with relatively high levels of turbulence, while for lower levels of turbulence  $CE$  may act differently. In any case, testable null hypotheses can be generated from these considerations. For instance, turbulence should not alter the growth rate of copepods because decreases in  $CE$  (through higher respiration or excretion caused by stress or otherwise) should balance increases in prey particle encounter probabilities. It would be most valuable if measurements of all terms were made in the same experiments and with the same organisms, overcoming technical and logistical difficulties. Actually, if the right parameters are chosen, only 2 of the 3 terms need to be measured while the third can be calculated from the equation. For exam-

ple, if ingestion and growth rates can be calculated from common units such as  $\mu\text{g C l}^{-1}$  (consumed and produced), then the terms are directly comparable and the  $CE$  directly obtained.

For the dinoflagellate data, other hypotheses could be derived. The present dataset, with all the limitations expressed above, shows a trend of a decrease in growth rate of these organisms under turbulent conditions. As mentioned above dinoflagellates could have peculiar physiological impediments to growth under turbulence. Will this decrease in growth rate also result in a decrease in nutrient uptake rate, or perhaps a decrease in growth efficiency, or both?

Overall, there are similarities between the effects of increased turbulence and temperature on planktonic organisms. Organisms tend to have an optimum temperature for growth and for ingestion, which may not match exactly (e.g. Choi & Peters 1992). Above these temperatures growth efficiencies tend to decrease, probably because respiration rates increase further than uptake or ingestion rates. Analogously, turbulence seems to increase uptake and ingestion rates (if food conditions are not saturating) through increased diffusion and encounter rates. Above a certain level, turbulence actually interferes with particle capturing processes and/or swimming behavior such as escape reactions of copepods (Marrasé et al. 1990, Saiz & Alcaraz 1992b, Hwang et al. 1994), probably resulting in lower growth efficiencies. Whether similar interferences could also occur in the case of nutrient uptake by non-motile osmotrophs is unknown. Finally, the dinoflagellates could present an altogether different response to turbulence or have much lower turbulence intensity threshold/optimum levels.

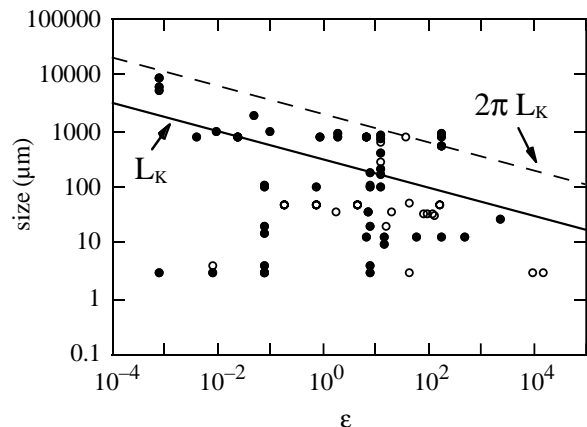


Fig. 6. Data points of organism size versus turbulence for experimental values that have a  $|rate_x| > 0.5$ . Lines show the Kolmogorov microscale as calculated with and without the  $2\pi$  coefficient. (●) Positive effects ( $rate_x > 0.5$ ); (○) negative effects ( $rate_x < -0.5$ )

### Size considerations

The experiments from the present dataset were performed predominantly with organisms smaller than  $L_K$ . Even when there are clear differences between the rate under turbulence and the rate under still water conditions, that is  $|rate_x| > 0.5$ , most of the organism sizes are below  $L_K$  (Fig. 6). If a factor of  $2\pi$  is applied to the calculation of  $L_K$  (as is sometimes done in the literature) then all but 4 of the data points fall below  $L_K$ . This means that many organisms can somehow sense, be affected by and/or respond to turbulence in a predominantly viscous environment, below the theoretical Kolmogorov microscale. A decade ago this statement would have raised strong controversy, at least from the theoretical point of view. Nowadays, it is accepted that the laminar shear field found at sub-eddy scales is the main hydrodynamic feature for explaining some of the experimental results (Shimeta et al. 1995, Karp-Boss et al. 1996).

There does not seem to be a pattern of preferential sizes being affected by turbulence. Both positive ( $rate_x > 0.5$ ) and negative ( $rate_x < -0.5$ ) effects of turbulence occur over most of the spectrum of organism sizes and correspond to an array of different taxa (Fig. 6). However, negative effects are dominated by dinoflagellates (53% of the cases), showing once more the strong growth rate response to turbulence for this group of organisms.

Organism size is not the only relevant lengthscale for turbulence to affect plankton. Phagotrophic organisms, such as copepods and fish larvae, have been shown to sense prey particles some distance away through optical, chemical or hydromechanical signals (Price 1988). In such cases, the sensing distance or a reaction distance to a sensed stimulus is important to determine how turbulence may alter encounter rates with prey. Different equations apply when such distance is above or below  $L_K$  (Rothschild & Osborn 1988, Kiørboe & Saiz 1995).

The relative average distance between individual particles, or mean free path (mfp), should also be important. A suspension of particles with a mfp greater than the  $L_K$  can see their encounter probability increased through the inertial motions of eddies even if the particles themselves are much smaller (Fig. 7). The mfp for a population of cells will depend on its concentration (Fig. 8). The mfp for bacteria, with a typical concentration in seawater between  $10^5$  and  $10^6$  cells  $ml^{-1}$ , will never be larger than the smallest eddies for a reasonable range of turbulence intensities. Small flagellated protozoa with characteristic oceanic concentrations of  $10^2$  to  $10^3$  cells  $ml^{-1}$  show larger mfps but would not intersect eddy sizes unless high turbulence conditions are met. For larger protozoa and algae, which

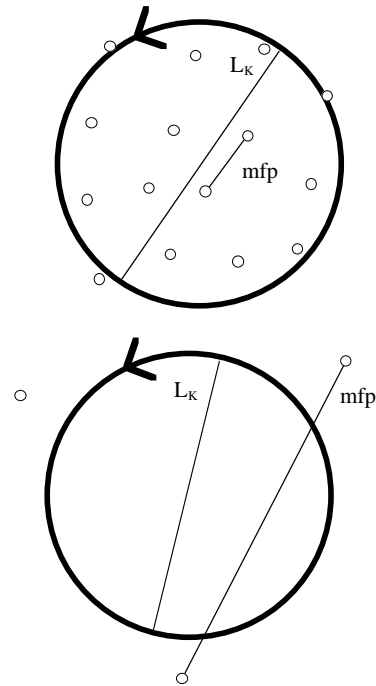


Fig. 7. Schematic representation of the relative size of the smallest eddies, which give the Kolmogorov microscale and the mean free path (mfp) between cells (O) depending on the concentration of cells

show even lower concentrations, the mfp tends to be larger than  $L_K$ , showing a potential for inertial-motion increased encounter for these organisms that could be important for mating, aggregation and other processes. For particles with concentrations lower than  $1 ml^{-1}$

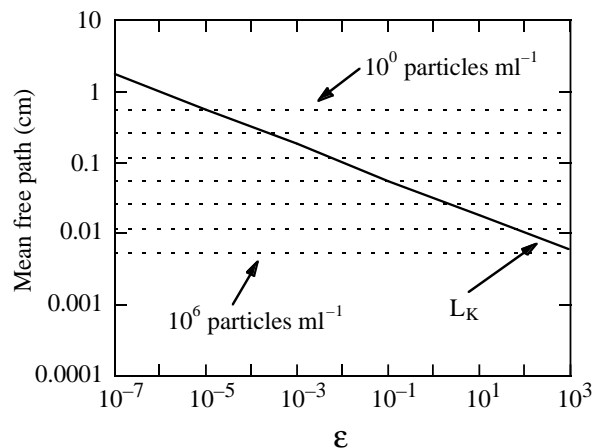


Fig. 8. Mean free path calculated for different plankton particle concentrations in a decadal increase (broken lines) compared to the Kolmogorov microscale for size. Three-dimensional mean free paths were calculated assuming a Poisson distribution of the particles with the formula  $mfp = 0.55N^{-1/3}$ , where  $N$  is the particle concentration

(typical of larger plankton) this discussion is not so relevant since their body sizes are already close to or above  $L_K$  and the encounter between those particles is already subjected to inertial motion.

When interacting particles are of different natures and sizes the picture becomes more complicated. Consider a predatory copepod with a reaction distance  $d$  smaller than  $L_K$  and a prey with a concentration so that the mfp  $> L_K$ . Using the terminology of Kiørboe & Saiz (1995), the encounter rate kernel due to turbulence should use a sub-Kolmogorov approach (their Eq. 2). However, since prey mfp  $> L_K$  it would seem that an inertial approach could still be applied (Eq. 3 of Kiørboe & Saiz 1995). The result is a higher theoretical encounter between prey and predator that better matches experimental data (Saiz & Kiørboe 1995). This means that both the reactive distance and the mfp between prey particles should be considered in determining the hydrodynamic range that is influencing encounter. When either  $d$  or prey mfps are larger than  $L_K$ , an inertial approach could be applied. mfps also become ecologically relevant for competing phytoplankton since they are one of the parameters for determining whether cells are directly competing (within and/or between species) for resources or are unaffected by their neighbors (Siegel 1998).

Another size-related consideration refers to the calculation of microscales. The Kolmogorov microscales apply to the momentum of a parcel of water. Scalars within this water mass will have diffusion characteristics that make them 'slower' to respond to the velocity/momentum field. This produces fluctuations of these scalars down to scales that are smaller than the Kolmogorov microscales. The Batchelor scale  $L_B$  (Tennekes & Lumley 1972) is defined for scalars analogous to the Kolmogorov microscale,

$$L_B = \left( \frac{D^2 \nu}{\epsilon} \right)^{1/4} \quad (7)$$

where  $D$  is the molecular diffusion of the scalar and has units of  $L^2 T^{-1}$ . These are the same units as those of kinematic viscosity, and one can think of viscosity as the molecular diffusion of momentum. In general  $D$  is smaller than  $\nu$ , and consequently  $L_B < L_K$ , meaning that the fluctuations of the scalars persist to smaller scales than the fluctuations in velocity (Table 3). This consideration is important for all osmotrophic organisms that may not sense momentum fluctuations but may be of the right size to take advantage of the fluctua-

Table 3. Diffusivities of different scalars in aqueous solution and the corresponding Batchelor lengthscale ( $L_B$ ). To calculate  $L_B$  a  $\nu$  of  $0.01 \text{ cm}^2 \text{ s}^{-1}$  and an  $\epsilon$  of  $10^{-3} \text{ cm}^2 \text{ s}^{-3}$  were used. For comparison, the Kolmogorov lengthscale ( $L_K$ ) would be 0.18 cm. BSA: bovine serum albumin

	Molecular weight	Diffusivity	Temperature	$L_B$ (cm)	Source
Heat	–	$1.5 \times 10^{-3}$	–	$6.89 \times 10^{-2}$	Mann & Lazier (1991)
Ammonium	18	$19.57 \times 10^{-6}$	25	$7.87 \times 10^{-3}$	Lide (1994)
Acetate	60	$10.89 \times 10^{-6}$	25	$5.87 \times 10^{-3}$	Lide (1994)
Nitrate	62	$19.02 \times 10^{-6}$	25	$7.76 \times 10^{-3}$	Lide (1994)
Glycine	75	$10.64 \times 10^{-6}$	25	$7.11 \times 10^{-3}$	Lide (1994)
Phosphate	95	$6.12 \times 10^{-6}$	25	$4.40 \times 10^{-3}$	Lide (1994)
Leucine	131	$8.74 \times 10^{-6}$	20	$5.26 \times 10^{-3}$	Confer & Logan (1991)
Glucose	180	$6.00 \times 10^{-6}$	20	$4.36 \times 10^{-3}$	Confer & Logan (1991)
Citrate	192	$6.23 \times 10^{-6}$	25	$4.44 \times 10^{-3}$	Lide (1994)
BSA	65000	$0.68 \times 10^{-6}$	–	$1.47 \times 10^{-3}$	Confer & Logan (1991)
Dextran	70800	$0.37 \times 10^{-6}$	–	$1.08 \times 10^{-3}$	Confer & Logan (1991)
20 nm particle	–	$0.22 \times 10^{-6}$	25	$5.90 \times 10^{-4}$	Boltzmann equation
0.5 $\mu\text{m}$ particle	–	$8.73 \times 10^{-9}$	25	$1.65 \times 10^{-4}$	Boltzmann equation
1 $\mu\text{m}$ particle	–	$4.37 \times 10^{-9}$	25	$1.16 \times 10^{-4}$	Boltzmann equation

tuations in a nutrient field. Consider a 100  $\mu\text{m}$  non-motile phytoplankter in an oligotrophic environment where nutrient uptake is diffusion-limited, that is, nutrient concentration is by definition 0 at the cell surface. Under a turbulence intensity of  $10^{-3} \text{ cm}^2 \text{ s}^{-3}$ ,  $L_K$  is 1800  $\mu\text{m}$ , much larger than the size of the organism, but  $L_B$  is 78  $\mu\text{m}$ , i.e., the fluctuations of the nutrient field in which the phytoplankter is living are of a scale similar to the cell itself. Since any fluctuation should produce concentrations larger than 0, the phytoplankter should be able to increase its uptake of nutrients.

Extensive theoretical and experimental research is still to be carried out before we can obtain a complete mathematical formulation or even a complete conceptual frame about the relevant size scales when considering the ecological particle interactions (predation and competition) and turbulence.

### Size is not all that matters

Organism physiology and much of ecology is governed by time-based rates. Hence, characteristic times of different abiotic and biotic processes should result in variables that may be important at certain scales for the life of organisms, while they may be unimportant at other scales.

Besides space, the Kolmogorov microscales are also defined for time and velocity (Fig. 2). These scales are representative of the turnover time and the velocity of the smallest eddies present at a certain energetic level. As with space, we can relate these microscales to scales characteristic of the plankton. For swimming organisms it seems obvious that their swimming speed

should determine their velocity scale. However, one can derive other velocities such as a sedimentation rate or a rising velocity through buoyancy mechanisms. Let us consider a spherical microflagellate of  $5 \times 10^{-4}$  cm in size swimming at  $2 \times 10^{-2}$  cm s<sup>-1</sup>. Under turbulence of  $10^{-3}$  cm<sup>2</sup> s<sup>-3</sup>, the Kolmogorov microscales for space and velocity are  $1.78 \times 10^{-1}$  cm and  $5.62 \times 10^{-2}$  cm s<sup>-1</sup> respectively. Thus, the microflagellate is much smaller than  $L_K$  and we would expect that the organisms would 'see' a non-fluctuating environment at any given moment. In contrast, the swimming speed of the microflagellate is of the same order of magnitude as the Kolmogorov microscale for velocity. This means that the organisms are not simply advected but that there must be an interaction between their swimming velocity vector and that of the smallest eddies, which should affect their behavior.

Organisms also have some characteristic time scales, including growth rate and generation time. Additionally, organisms that ingest particles will have a characteristic time between ingestion events, or successful

particle retention events, or particle detection events. For osmotrophic organisms, similar approaches can give average times between the uptake of 2 molecules. Of course, in both cases, uptake or ingestion events can occur simultaneously for more than 1 molecule or particle, which requires more complicated calculations. Table 4 shows a summary of characteristic scales for different planktonic organisms.

For phagotrophs, considering the maximum (generation time) or minimum organism time scale (e.g., time between particle captures) does not make much difference since the organisms will always experience fluctuations during their characteristic time scale (Fig. 9) but for the lowest energetic conditions (below  $10^{-6}$  cm<sup>2</sup> s<sup>-3</sup>). In the case of osmotrophs, the span between the shortest and longest time scales is much wider. Effects of turbulence should then be scaled to the relevant overall time scale for the organism (somewhere in between the 2 extreme time scales), which will determine whether the cells will or will not experience fluctuations in the nutrient field within that relevant time scale (Fig. 9).

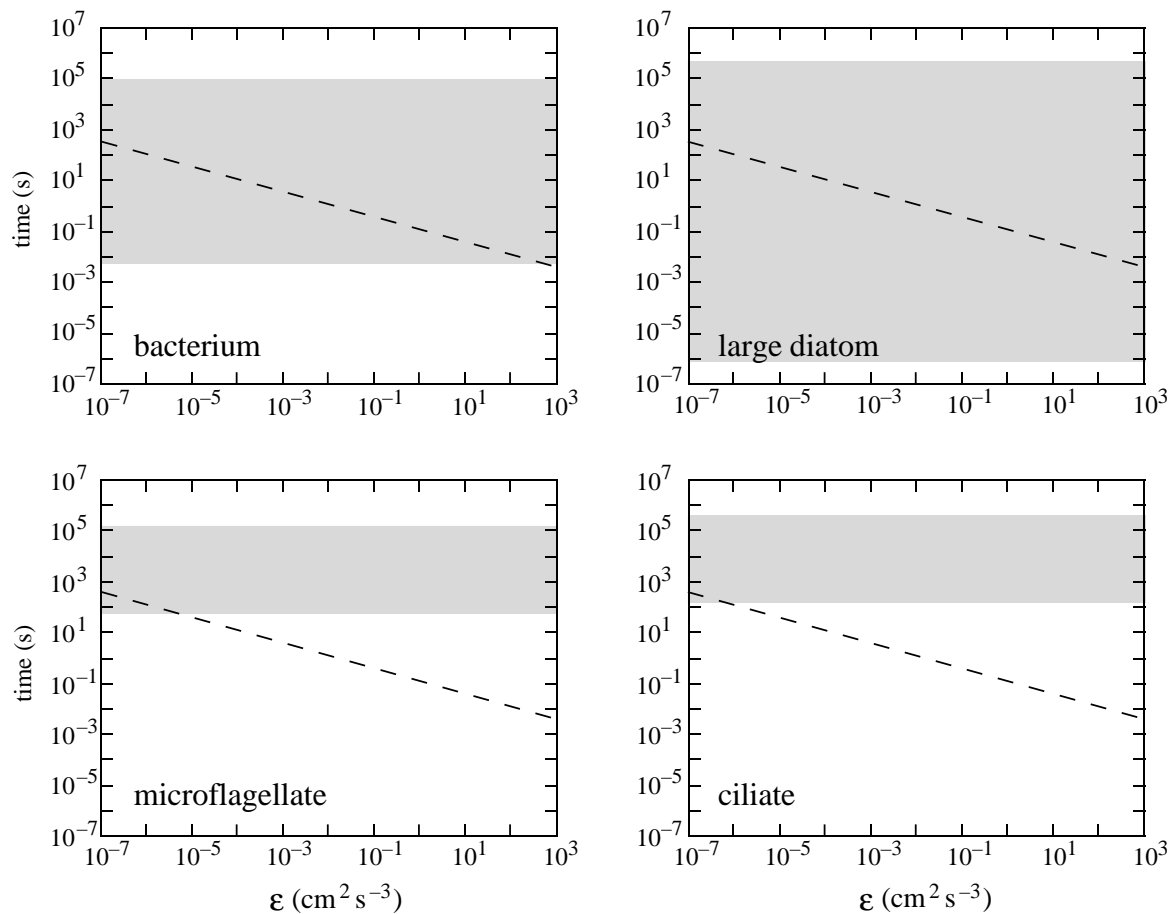


Fig. 9. Characteristic time scales for different planktonic organisms. Shaded areas are delimited by the maximum and the minimum time scales. Broken line shows the Kolmogorov microscale for time



Table 4. Characteristic size, velocity and time scales of several typical planktonic organisms

Organism	Size (cm)	Prey size (cm)	Generation time (s)	Characteristic process time (s)	Swimming velocity (cm s <sup>-1</sup> )
Microflagellate	$5 \times 10^{-4}$	$0.5 \times 10^{-4}$	$1.7 \times 10^5$	70 <sup>a</sup>	0.02
Ciliate	$50 \times 10^{-4}$	$5 \times 10^{-4}$	$4.3 \times 10^5$	170 <sup>a</sup>	0.1
Copepod	0.1	$10 \times 10^{-4}$	$4.3 \times 10^{5b}$	0.17 <sup>a</sup>	0.4
Fish larva	1	0.015	$1.3 \times 10^{6b}$	4.4 <sup>a</sup>	1.5
Bacterium	$0.5 \times 10^{-4}$	–	$8.6 \times 10^4$	$6 \times 10^{-3c}$	0.003
Small diatom	$10 \times 10^{-4}$	–	$8.6 \times 10^4$	$6 \times 10^{-6d}$	–
Dinoflagellate	0.003	–	$2.6 \times 10^5$	$4 \times 10^{-7d}$	0.02
Large diatom	0.01	–	$4.3 \times 10^5$	$9 \times 10^{-7d}$	–

<sup>a</sup>Calculated from organism and prey size, and generation time, and assuming a 40% volume conversion efficiency  
<sup>b</sup>Time for duplication of biomass  
<sup>c</sup>Average time between uptake of 2 molecules of phosphorus-phosphate. Calculated from organism size, carbon-to-volume conversion factors (Bjornsen 1986), a C:P = 80, and the generation time  
<sup>d</sup>Average time between uptake of 2 molecules of phosphorus-phosphate. Calculated from organism size, carbon-to-volume conversion factors (Montagnes et al. 1994), a C:P = 106, and the generation time

## CONCLUSIONS

Turbulence levels used in experiments with plankton seem to be, in general, higher than levels measured in the ocean. Efforts are being made to reduce the intensity of turbulence in biological experiments, to more accurately measure and estimate turbulence in these experiments and to obtain oceanic turbulence measurements under stormy conditions and near the surface of the ocean, which will bring field and laboratory data closer together.

Biological rates related to ingestion of particles or uptake of dissolved substances are, on average, favored by turbulence but there is considerable variability related to taxa and organism sizes. Growth rates show a different response to turbulence depending on the taxa; while in general there is no trend, dinoflagellates show a strong negative effect of turbulence.

The calculation of  $L_K$  from oceanic turbulence measurements shows that most planktonic organisms are unlikely to experience eddy-like motion. Nevertheless, the experimental data obtained so far show that even organisms with lengthscales 1000 times smaller than the Kolmogorov microscale can be affected by turbulence (probably by the remaining laminar shear field). Additionally, organism size is not the only relevant lengthscale to determine whether a certain turbulence level can affect an organism or not.  $L_B$ , reactive distances and the mfp between particles are additional length scales to be considered in certain situations. Scales with other dimensions such as time and velocity may also be important when compared to characteristic values for organisms, especially for time-dependent processes and when considering population dynamics.

We still need many more experimental results and integrating theoretical formulations to discern which scales are relevant for turbulence to affect planktonic organisms, and in what situations they are relevant. We hope that this review has given a glimpse of trends that are starting to appear as well as a baseline to construct a testable hypothesis. Finally, communities and systems may show characteristic behaviors and responses to turbulence that can not be derived from the sum of effects on the different taxa composing the community (Estrada et al. 1987, Peters et al. 1998, or Petersen et al. 1998). If our ultimate objective is to understand the effects of turbulence at the community or system level, there is a great need for experiments at these levels.

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