

Microscale processes in the ocean: why are they so important for ecosystem functioning?

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Abstract : Turbulence has widely been regarded as being a homogeneous process. Turbulence effects on ecosystem fluxes have been estimated from the mean values of turbulent kinetic energy dissipation rates. However, turbulent processes are highly intermittent. Making use of multifractal concepts, this study shows that the intermittent nature of microscale turbulence results in (i) an increase in the rate of nutrient fluxes around non-motile phytoplankton cells (6-62%), (ii) a decrease in the physical coagulation of phytoplankton cells (25-48%) and in the subsequent phytoplankton aggregate volumes (22-41%), and (iii) a decrease of the turbulence contribution to predator-prey encounter rates (25-50%).

Key words : *microscale turbulence, intermittency, nutrient fluxes, physical coagulation, predator-prey encounter rates, phytoplankton and zooplankton dynamics, matter fluxes*

1. Introduction

There has been a long lasting interest among plankton ecologists to quantify the effects of microscale turbulence on both phyto- and zooplankton trophodynamics. Knowledge of such processes (and their space-time variability) is a prerequisite for understanding trophic interactions in the pelagic environment and the functioning of plankton food webs. Turbulence has thus been shown to play a salient role in determining the rates of nutrient fluxes around phytoplankton cells (ESTRADA and BERDALET, 1997), the formation of phytoplankton aggregates (JACKSON, 1994), the subsequent vertical matter fluxes in the ocean (KIORBOE *et al.*, 1990), and the predator-prey encounter rates (ROTHSCHILD and OSBORN, 1988).

Microscale turbulent processes have been widely regarded as homogenizing factors. Modeling of nutrient fluxes (LAZIER and MANN, 1989; KARP-BOSS *et al.*, 1996), aggregation processes (KIORBOE *et al.*, 1990), predator-prey encounter rates and studies of zooplankton

trophodynamics (e.g. KIORBOE and SAIZ, 1995; CAPARROY and CARLOTTI, 1996) have thus implicitly assumed that microscale zooplanktonic and phytoplanktonic distributions are statistically homogeneous in space and time.

However, an intriguing aspect of microscale turbulence is that it may generate microscale patchiness rather than uniformity (JIMENEZ, 1997). Instantaneous gradients of scalars such as temperature, salinity or nutrients are indeed the greatest at scales similar to the Kolmogorov microscale, i.e. the viscous scale where viscosity effects cannot be neglected and start to smooth out turbulent fluctuations (SANFORD, 1997). In other words, this form of variability, or "intermittency", reflects heterogeneous distributions with a few high density patches and a wide range of low density patches (Fig. 1), and has now widely been characterized in terms of physical, chemical and biological structures. More specifically, these fluctuations have been analyzed in the multifractal framework (PASCUAL *et al.*, 1995; SEURONT, 1997, 1999a, b; SEURONT *et al.*, 1996a, b, 1999, 2001a, b), with statistical tools that are more general than standard methods, such as spectral techniques, which only provide limited information on the statistics of the process due to their intrinsic

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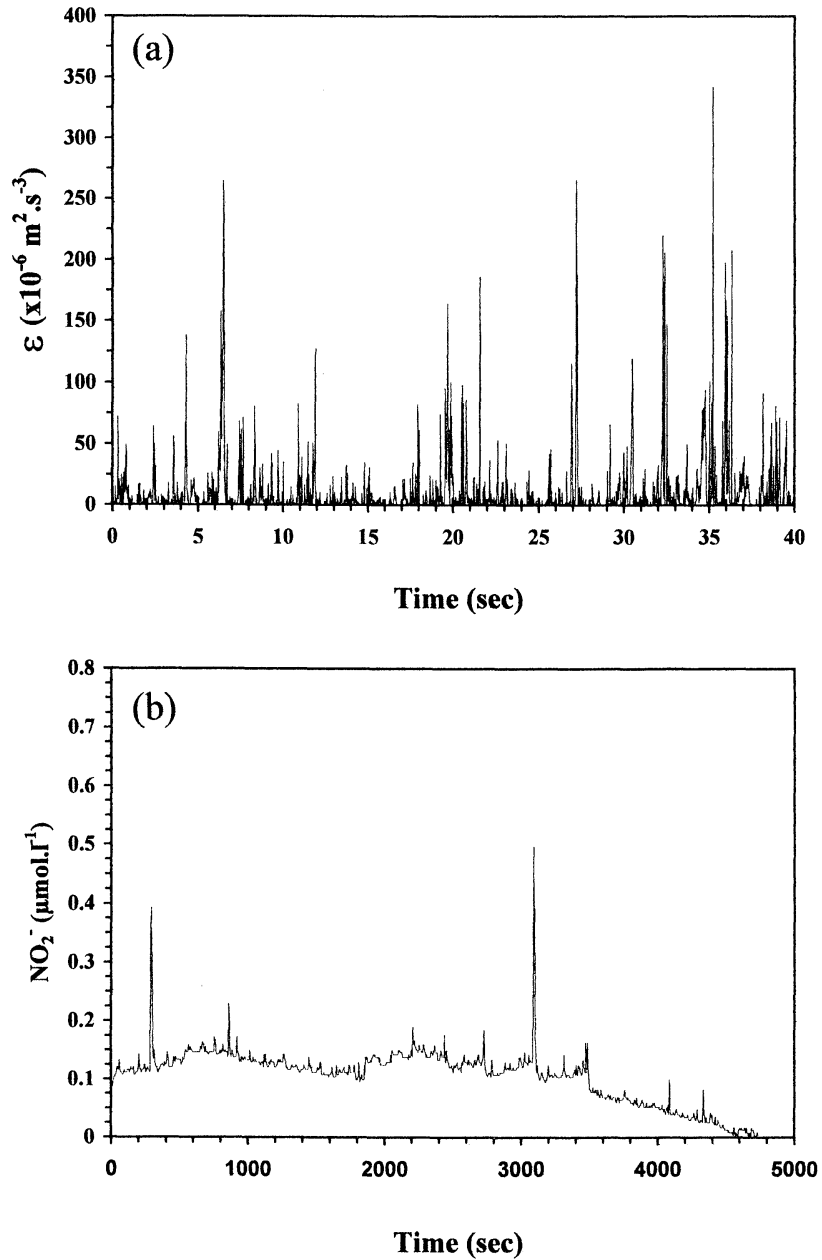


Fig. 1. Samples of (a) the pattern of the turbulent kinetic energy dissipation rates estimated from grid generated turbulent velocity fluctuations recorded with a hot wire velocimeter (redrawn from SEURONT *et al.*, 1999), and (b) the high frequency distribution of nitrite NO_2^- recorded in the Eastern English Channel (redrawn from SEURONT *et al.*, 2001a). Turbulent kinetic energy dissipation rates and nitrite distributions exhibit at all scales sharp fluctuations called intermittency.

links to Gaussian distributions (see e.g. PLATT and DENMAN, 1975; FASHAM, 1978).

As microscale physical processes are of primary interest in plankton ecology (e.g. DAVIS *et al.*, 1991), the question addressed here is whether these specific intermittent physical structures affect marine life and its associated fluxes. To that end, in the present paper I (i) review briefly the formalism developed by SEURONT *et al.* (2001b) to describe the statistical behavior of intermittent turbulent processes, (ii) use this approach to derive simple equations used to estimate the effect of intermittent microscale turbulence on nutrient fluxes around non-motile phytoplankton cells, on phytoplankton cells aggregations, and on predator-prey encounter rates, and (iii) quantify the potential specific effects of intermittent microscale turbulence on these processes.

2. Describing microscale intermittent processes in the ocean

In this paper I only review the main properties of a multifractal field. More details on the use of multifractal algorithms to marine ecology studies, and what can be concluded from their use can be found in SEURONT *et al.* (1999). A main property of a multifractal field is that its fluctuations are not destroyed by smoothing at any scale, until the outer scale of the system is reached. For a given turbulent energy dissipation rate ε , this means that the multifractal field ε averaged over a scale l will have a scale-dependent value denoted as ε_l , or as ε_λ . Here we introduce a non-dimensional scale ratio λ ($\lambda = L/l$), which is the ratio between an external length scale L and a targeted length scale within the inertial subrange, i.e. $L \leq l \leq l_K$ where the Kolmogorov length scale is expressed as l_K [see SEURONT *et al.* (1999) for further details]. We assume in this analysis $\lambda \gg 1$. The scale-dependent multifractal field ε_λ can be described by its probability distribution, or equivalently, by its statistical moments $\langle\langle \varepsilon_\lambda^q \rangle\rangle$, where we consider any $q \geq 0$. These moments can be scaled with the scale ratio λ , as (SEURONT *et al.*, 1999):

$$\langle\langle \varepsilon_\lambda^q \rangle\rangle = \varepsilon_0^q \lambda^{K(q)} \quad (1)$$

where ' $\langle\cdot\rangle$ ' indicates statistical or spatial

averaging, $\varepsilon_0 = \langle \varepsilon \rangle$ is the mean of the multifractal process ε_λ , and $K(q)$ is a scale-invariant moment function which is convex and satisfies $K(0) = 0$ and $K(1) = 0$. The knowledge of $K(q)$ fully describes the statistics of the process, in an equivalent manner as the probability distribution. The second moment $\mu = K(2)$ is usually denoted as an intermittency parameter. In the following we consider a continuous range of values of $q \geq 0$. It should be noted here that Eq. (1) is valid only for scales belonging to the inertial subrange, thus for $l \leq \lambda \leq \Lambda$, where $\Lambda = L/l_K$ is the maximum scale ratio, between the larger outer scale and the Kolmogorov scale l_K .

Subsequently, Eq. (1) can be used to evaluate the average of any polynomial function $f(\varepsilon_\lambda)$ of the multifractal field ε_λ as (SEURONT *et al.*, 2001b):

$$f(\varepsilon_\lambda) = \sum_{p=0}^N a_p (\varepsilon_\lambda)^p \quad (2)$$

where a_p are constants, and p the polynomial order of the function $f(\varepsilon_\lambda)$. Averaging the function finally leads to:

$$\langle f(\varepsilon_\lambda) \rangle = \sum_{p=0}^N a_p \varepsilon_0^p \lambda^{K(p)} \quad (3)$$

This equation will be used in the following section.

3. Significance of microscale intermittency

To evaluate the potential significance of intermittency for nutrient fluxes around non-motile phytoplankton cells, phytoplankton cells aggregations, and predator-prey encounter rates we need to compare the conventional view of homogeneous turbulence and the effects of intermittency.

3.1 Intermittent turbulence and nutrient fluxes around phytoplankton cells

Following KARP-BOSS *et al.* (1996), the increased rate of nutrient flux due to turbulence around non-motile phytoplankton cells can be directly estimated using the Sherwood number, Sh , as:

$$Sh_1 = 1 + 0.29 \frac{r}{(D\nu^{-1/2})^{1/2}} \cdot \frac{1}{\varepsilon_0^{1/4}} \quad \text{for } r < l_B \quad (4)$$

$$Sh_2 = 0.55 \frac{r}{(D\nu^{-1/2})^{1/2}} \cdot \frac{1}{\varepsilon_0^{1/6}} \quad \text{for } r > l_B \quad (5)$$

where r is the cell radius (m), D the diffusivity ($D = 10^{-9} \text{m}^2 \cdot \text{s}^{-1}$), ε_0 the mean turbulent energy

dissipation rate ($\text{m}^2 \cdot \text{s}^{-3}$), ν the kinematic viscosity ($\nu = 10^{-6} \text{m}^2 \cdot \text{s}^{-1}$) and l_b the Batchelor microscale, the scale of the smallest variations in the ambient nutrient field. One may note here that the Batchelor microscale l_b is smaller than the Kolmogorov microscale l_K following $l_K = l_b (D/\nu)^{1/2}$.

Now let the turbulent kinetic energy dissipation rate ε be a multifractal variable ε_λ characterized by the scaling moment function $K(q)$ defined above, and by its mean $\varepsilon_0 = \langle \varepsilon_\lambda \rangle$. Consider the average Sherwood numbers Sh_1' and Sh_2' associated to the intermittent (multifractal) variable ε_λ and defined as $Sh_1' = \langle Sh_1(\varepsilon_\lambda) \rangle$ and, $Sh_2' = \langle Sh_2(\varepsilon_\lambda) \rangle$ when $r < l_b$ and $> l_b$, respectively. Using Eq. (3), Eqs. (4) & (5) can thus be rewritten as:

$$Sh_1 = 1 + 0.29 \frac{r}{(D\nu^{-1/2})^{1/2}} \cdot \frac{1}{\varepsilon_0^{1/4} \lambda^{K(1/4)}} \quad \text{for } r < l_b \quad (6)$$

$$Sh_2' = 0.55 \frac{r}{(D\nu^{-1/2})^{1/2}} \cdot \frac{1}{\varepsilon_0^{1/4} \lambda^{K(1/6)}} \quad \text{for } r > l_b \quad (7)$$

One needs to be aware that $\lambda \gg 1$ while $K(1/4) < 0$ and $K(1/6) < 0$, therefore $1/\lambda^{K(1/4)}$ and $1/\lambda^{K(1/6)}$ act as enhancing factors in Eqs. (6) & (7) yielding $(Sh_1'/Sh_1) > 1$ and $(Sh_2'/Sh_2) > 1$. This shows that using a mean value of the turbulent kinetic energy dissipation rate ε_0 instead of the multifractal distribution ε_λ leads to underestimate the turbulence contribution to the rates of nutrient fluxes around phytoplankton cells, whatever their size may be.

In order to quantify this difference, one needs to estimate the intermittent enhancing factors (Sh_1'/Sh_1) and (Sh_2'/Sh_2) due to $1/\lambda^{K(1/4)}$ and $1/\lambda^{K(1/6)}$ in Eq. (6) & (7) using realistic values of λ , $K(1/4)$ and $K(1/6)$. The inertial subrange scale ratio λ is increasing with increasing intensities of turbulence, and can be reasonably regarded as ranging between 10^2 and 10^5 (e.g. GREGG, 1999). The scale-invariant moment exponents $K(1/4)$ and $K(1/6)$ have been estimated from high resolution shear vertical profiles recorded in tidally mixed coastal waters following SEURONT *et al.* (1999) as $K(1/4) = -0.053 \pm 0.005$ and $K(1/6) = -0.042 \pm 0.004$ (SEURONT and YAMAZAKI, unpublished data). The resulting enhancing factors $(Sh_1'/$

$Sh_1)$ and (Sh_2'/Sh_2) ranges between 1.06 and 1.19, and between 1.21 and 1.62 when $r < l_b$ and $r > l_b$, respectively. That finally leads to consider an increase in the rate of nutrient fluxes around phytoplankton cells due to microscale turbulence intermittency ranging between 6.26% and 19.07% for phytoplankton cells smaller than the Batchelor microscale l_b , and between 21.22% and 61.78% for phytoplankton cells larger than the Batchelor microscale l_b . One may also note that the inertial subrange scale ratio increases with increasing intensities of turbulence. The increase in the rate of nutrient fluxes around phytoplankton cells of any size is thus higher when the intensity of turbulence is high.

3.2 Intermittent turbulence and physical coagulation of phytoplankton cells

Theoretical analyses of particles coagulation processes predict that aggregate formation depends on the probability of particle collision and on the efficiency with which two particles that collide and stick together afterwards (MCCAVE, 1984; JACKSON, 1990). The former is a function of particle concentration, size and the mechanism by which particles are brought into contact, e.g. Brownian motion, shear or the differential settlement of particles. The latter which is not studied in the present paper depends mainly on the physicochemical properties of the particle surface and may vary with the particle type.

Let consider a monospecific phytoplankton cells suspension characterized by a cell radius r (m) and cell concentration C ($\text{cells} \cdot \text{m}^{-3}$). Because all particles are of the same size and density and settle with the same velocity, and because encounters due to Brownian motion is insignificant for particles $> 1 \mu\text{m}$ (MCCAVE, 1984), the only mechanism that may increase the relative velocity between phytoplankton cells and thus bring them to collide is due to turbulent shear and can be expressed as (KIORBOE, 1997):

$$E_1 = 10.4r^3C^2 (\varepsilon_0/\nu)^{1/2} \quad (8)$$

where E_1 is the encounter rate due to turbulence ($\text{encounter} \cdot \text{s}^{-1}$), ε_0 the mean turbulent energy dissipation rate ($\text{m}^2 \cdot \text{s}^{-3}$) and the kine-

matic viscosity ($\nu = 10^{-6} \text{m}^2 \cdot \text{s}^{-1}$).

As previously done in section 3.1, let the turbulent kinetic energy dissipation rate be a multifractal variable ε_λ characterized by the scaling moment function $K(q)$ defined above, and by its mean $\varepsilon_0 = \langle \varepsilon_\lambda \rangle$. Here, E_1 and $E_1' = E(\varepsilon_0)$ are regarded as estimates of average encounter rates, i. e. $E_1 = E(\varepsilon_0)$ and $E_1' = \langle E(\varepsilon_\lambda) \rangle$ when the turbulent energy dissipation rates are regarded as homogeneous and intermittent (multifractal) variables, respectively. In this case, Eq. (8) is rewritten as:

$$E_1' = 10.4r^3C^2 \nu^{-1/2} \varepsilon_0^{1/2} \lambda^{K(1/2)} \quad (9)$$

This finally yields:

$$E_1' = E_1 \lambda^{K(1/2)} \quad (10)$$

and as defined above, $\lambda \gg 1$ and $K(1/2) < 0$, $\lambda^{K(1/2)}$ thus acts as a restraining factor therefore $E_1' < E_1$. Using the values of λ proposed in section 3.1 (i.e. $\lambda \in [10^2, 10^5]$) and $K(1/2) = -0.063 \pm 0.005$ (SEURONT and YAMAZAKI, unpublished data), the factor $\lambda^{K(1/2)}$ ranges between 0.48 and 0.75. Now, taking into account the intermittent nature of microscale turbulence leads to consider a decrease in its contribution to the physical coagulation of phytoplankton cells ranging between 25% and 48%. This decrease is higher when the turbulence levels are high (i.e. the inertial subrange scale ratio is large).

Considering the role played by large particle aggregates in the vertical flux of organic matter in the ocean (GARDNER, 1997; JACKSON and BURD, 1998), I focus the effects of this decrease in encounters due to intermittency on the growth in particle size. It has been shown that the average solid volume of aggregates increases according to the following formula (KIORBOE *et al.*, 1990):

$$V_t = V_0 e^{\alpha [7.8\phi(\varepsilon_0/\nu)^{1/2}/\pi] t} \quad (11)$$

where V_0 and V_t are the average volume of aggregates at time 0 and t , α is the stickiness coefficient (i.e. $\alpha \in [0, 1]$), ϕ is the volume-concentration of cells [$\phi = (4/3) \pi r^3 C_0$]. Introducing the precise statistical distributions of turbulent dissipation rate ε_λ in Eq. (11) instead of its average value ε_0 leads to a decrease in the aggregate average volumes ranging

between 22% and 41% in low and high hydrodynamic conditions, respectively.

3.3 Intermittent turbulence and zooplankton trophodynamics

Following the seminal theory of ROTHSCHILD and OSBORN (1988), KIORBOE and SAIZ (1995) demonstrated that the encounter rate E (encounters. s^{-1}) between plankton predators and preys can be expressed as the sum of the encounter rate due to organism behavior and the encounter rate due to microscale turbulence. The former is a function of particle concentration, swimming speed of predator and prey and perceptive distance of the predator. The latter which I explore here in more details is expressed as:

$$E_2 = C \pi R^2 w \quad (12)$$

where E_2 is the encounter rate due to microscale turbulence, C is the number of preys per unit volume (preys. m^{-3}), R is the perceptive distance of the predator (m), and w ($\text{m} \cdot \text{s}^{-1}$) is the root-mean-square turbulent velocity enhancing the relative motion between predator and prey. The rms turbulent velocity w is directly related to the intensity of turbulence, characterized by a mean value of the turbulent kinetic energy dissipation rate ($\text{m}^2 \cdot \text{s}^{-3}$) following (ROTHSCHILD and OSBORN, 1988):

$$w = 1.9 (\varepsilon_0 d)^{1/3} \quad (13)$$

where d is the separation distance between predator and prey when encounter takes place, i.e. $d = R$ (e.g. VISSER and MACKENZIE, 1998). Finally, inserting the expression for the rms turbulent velocity [Eq. (13)] in Eq. (12) yields:

$$E_2 = 1.9C \pi R^{7/3} \varepsilon_0^{1/3} \quad (14)$$

Let now ε_λ be a multifractal variable characterized by the scaling moment function $K(q)$ defined above, and by its mean $\langle \varepsilon_\lambda \rangle = \varepsilon_0$. Here, E_2 and E_2' are the estimates of average encounter rates due to turbulence, i.e. $E_2 = E(\varepsilon_0)$ and $E_2' = \langle E(\varepsilon_0) \rangle$ when the turbulent energy dissipation rates are regarded as homogeneous and intermittent (multifractal) variables, respectively. Eq. (14) can thus be rewritten as:

$$E_2' = 1.9C \pi R^{7/3} \varepsilon_0^{1/3} \lambda^{K(1/3)} \quad (15)$$

Now $E_2' = E_2 \lambda^{K(1/3)}$, and as defined above, $\lambda \gg 1$ and $K(1/3) < 0$, $\lambda^{K(1/3)}$ acts as a restraining factor therefore $E_2' < E_2$. Considering values of the inertial subrange scale ratio bounded between 10^2 and 10^3 (e.g. GREGG, 1999), and $K(1/3) = -0.060 \pm 0.003$ (SEURONT and YAMAZAKI, unpublished data), the factor $\lambda^{K(1/3)}$ ranges between 0.50 and 0.76. Taking into account the intermittent structure of turbulent kinetic energy dissipation rate ε_λ instead of an average value ε_0 then decreases the contribution of microscale turbulence to the predator-prey encounter rate of 25% to 50% for ε_0 values ranging from 10^{-10} to $10^{-2} \text{ m}^2 \cdot \text{s}^{-3}$, GREGG, 1999).

4. Discussion and Conclusions

The estimated increase in the rate of nutrient fluxes around non-motile phytoplankton cells (ranging from 6 to 62%) and the decrease in the effects of microscale turbulence on physical coagulation of phytoplankton in an intermittent turbulence condition (ranging from 25% to 48%) could be of prime interest in the general understanding of primary production as well as more general nitrogen and carbon cycling studies.

The strongest rates of nutrient fluxes observed in high turbulent conditions (i.e. up to 62%) could indeed provide a potential phenomenological explanation to the persistence of local high phytoplankton diversity in highly energetic areas referred as the 'paradox of the plankton' (HUTCHINSON, 1961). This hypothesis is supported by Eqs. (6) & (7) which demonstrate that intermittency effects on nutrient fluxes are higher for large phytoplankton cells [21–62%; cf. Eq. (7)] than for smaller ones [6–19%; cf. Eq.(6)], large and small phytoplankton species being respectively characteristic of highly dissipative and still water environments (e.g. MARGALEF, 1997).

On the other hand, the decreased physical coagulation shown here is associated with a decrease in phytoplankton aggregate size (22% to 41%). This change in the growth dynamics of aggregate size due to coagulation directly leads to a weaker enhancement of Stokes' settling velocities and, hence, to decreased vertical fluxes of phytoplankton. As a consequence, the CO_2 storage capacity of the deep ocean

could be weaker than previously thought, and lead to salient effects on carbon cycling estimates between ocean and atmosphere. Consider, for instance, that only 50% of the 22–41% decrease in aggregate size leads to a decrease in the vertical phytoplankton flux, then the deep ocean CO_2 storage capacity could be decreased by 10–20%.

More generally, considerations of the intermittent nature of microscale turbulence could be regarded as a potential new way to improve estimates of key fluxes, such as primary, new and regenerated productions. These estimates are still disputed to within a factor of 10 (see e.g. PLATT *et al.* 1989), mainly because of our limited capacity to harmonize the different measurement procedures and their implied time and space scales (BERGER 1989 : PLATT *et al.* 1989), but also because of the extreme sensitivity of actual numerical modeling, even to minor changes in parameter values (WERNER *et al.* 1993).

In the case of predator-prey interactions, the results presented here indicate a decreased contribution of intermittent microscale turbulence in predator-prey encounter rates ranging between 25% and 50% in low and high hydrodynamic conditions, respectively. Following the likewise relative inadequacy observed between theoretical encounter theory and empirical result of zooplankton grazing in turbulent environment (e.g. DOWER *et al.*, 1997), a new hypothesis for zooplankton trophodynamics [extensively explored elsewhere (SEURONT *et al.*, 2001b)], can be suggested on the basis of different biological and ecological observations. First, zooplankton swimming speeds can overcome local turbulent velocity fluctuations (YAMAZAKI and SQUIRES, 1996), and then become independent of their surrounding physical turbulent environment. Second, microscale phytoplankton distributions are very patchy both in low and high turbulence conditions (JAFFE *et al.*, 1998 : SEURONT *et al.*, 1996a, b, 1999), and result from complex interactions involving turbulence intensity, phytoplankton physiological state and phytoplankton assemblages specific composition (SEURONT, 1999 : SEURONT *et al.*, 2001a). Third, planktonic predators such as copepods present different

behavioral adaptations to food patchiness such as reduced motility in food patches (e. g. BUNDY *et al.*, 1993). Finally, as suggested by their chemosensory abilities (e.g. DOAL *et al.*, 1998; STRICKLER, 1998), planktonic predators can reasonably be regarded as being able to locate food patches and to move from one high density patch to another. Based on these arguments, the phytoplankton distribution experienced by planktonic predators is skewed toward a limited area. The observed increased ingestion under turbulent conditions could then be the results of an active exploitation of food patchiness by predators rather than a direct consequence of an increased predator-prey encounter rates by turbulence. Also, this hypothesis could explain the discrepancy observed by SAIZ (1994) between empirical encounter rates and the theoretical values expected using ROTHSCHILD and OSBORN theory.

Taking both the coherent nature of turbulence at the scale of planktonic organisms, and the individual behavior of plankton organisms (KEIYU *et al.*, 1994), this article provides a general theoretical approach for testing the potential effects of intermittent distributions on ocean fluxes, and could also be advantageously coupled with recent modeling approaches for individual adaptations to heterogeneously distributed resources (RAMAT *et al.*, 1998; SEURONT *et al.*, 2001b).

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