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# Turbulence intermittency, small-scale phytoplankton patchiness and encounter rates in plankton: where do we go from here?

Laurent Seuront<sup>a,\*</sup>, François Schmitt<sup>b</sup>, Yvan Lagadeuc<sup>a,2</sup>

<sup>a</sup>Station Marine de Wimereux, CNRS UPRES-A 8013 ELICO, Université des Sciences et Technologies de Lille, BP 80, F-62930 Wimereux, France

<sup>b</sup>Department of Fluid Mechanics, VUB, Pleinlaan 2, B-1050 Brussels, Belgium

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## Abstract

Turbulence is widely recognized to enhance contact rates between planktonic predators and their prey. However, previous estimates of contact rates are implicitly based on homogeneous distributions of both turbulent kinetic energy dissipation rates and phytoplanktonic prey, while turbulent processes and phytoplankton cell distributions have now been demonstrated to be highly intermittent even on small scales. Turbulent kinetic energy dissipation rates and intermittent (i.e. patchy) phytoplankton distributions can be wholly parameterized in the frame of universal multifractals. Using this framework and assuming statistical independence between turbulent kinetic energy dissipation rate and phytoplankton distributions, we evaluated the effect of intermittent turbulence and the potential effects of zooplankton behavioral responses to small-scale phytoplankton patchiness on predator–prey encounter rates. Our results indicated that the effects of turbulence on predator–prey encounter rates is about 35% less important when intermittently fluctuating turbulent dissipation rates are considered instead of a mean dissipation value. Taking into account zooplankton behavioral adaptations to phytoplankton patchiness increased encounter rates up to a factor of 60. © 2001 Published by Elsevier Science Ltd.

*Keywords:* Phytoplankton; Zooplankton; Oceanic turbulence; Intermittency; Encounter rate estimates; Behavior

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\* Corresponding author. Fax: + 81-3-5463-0379.

E-mail address: laurent@tokyo-u-fish.ac.jp (L. Seuront).

<sup>1</sup> Present address: Ocean Ecosystem Dynamics Laboratory, Department of Ocean Sciences, Tokyo University of Fisheries, 4-5-7 Konan, Minato-ku, Tokyo 108-8477, Japan.

<sup>2</sup> Present address: Université de Caen, IUT, Bd du Maréchal Juin, F-14032 Caen cedex, France.

## 1. Introduction

The influence of small-scale turbulence on predator–prey interactions in plankton has received a great deal of attention in recent years. Much of this attention stems from the seminal work of Rothschild and Osborn (1988), who proposed an enhanced rate of predator–prey contact due to small-scale turbulent shear. Subsequently, much has been written about the positive influences of turbulence on predator–prey encounter and potential negative influences of turbulence on organism behavior (MacKenzie et al., 1994; Dower et al., 1997). In any case, because small-scale turbulent processes have been regarded as homogenizing factors, modeling of predator–prey contact rates and studies of plankton trophodynamics have implicitly assumed that both zooplanktonic and phytoplanktonic distributions are random in space and time (e.g. Sundby and Fossum, 1990; MacKenzie and Leggett, 1991; Kiørboe and Saiz, 1995; Caparroy and Carlotti, 1996).

An intriguing aspect of small-scale turbulence, however, is that it may promote small-scale patchiness rather than uniformity (Jimenez, 1997; Jou, 1997). Instantaneous gradients of scalars such as temperature, salinity or nutrients are indeed 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 (Gargett, 1997; Sanford, 1997). Thus we occasionally should expect stronger bursts than expected in a non-intermittent, homogeneous turbulence, which accentuate the skewness (i.e. asymmetry) of a given probability distribution, causing it to deviate from Gaussianity (in which case the skewness is nil, and the probability distribution symmetric). In other words, this form of variability reflects heterogeneous distributions with a few dense patches and a wide range of low-density patches. Recent empirical studies conducted in highly turbulent environments have hence shown that both physical and biological parameters such as temperature, salinity, and phytoplankton biomass were neither homogeneously nor randomly distributed, but rather exhibited very specific heterogeneous distributions, even on smaller scales (Seuront et al., 1996a, b; 1999).

Such heterogeneous distributions could be a salient issue for the general understanding of pelagic ecosystem functioning. Davis et al. (1991) showed that the feeding and growth rates of larval fish increased when the larvae were capable of finding and remaining within food patches, perhaps via some kind of area-restricted searching strategy, i.e. increased rate of turning once food has been encountered (Timbergen et al., 1967). Subsequently, Yamazaki (1993) propounded that “plankton organisms experience the local flow structure of turbulence, not the average of the flow field” because turbulence presents strong organization in both space and time. In such a context, if copepods are able to move from one dense patch to another, then they experience a local phytoplanktonic field more dense than the average. Changes in copepod behavior could thus be the response to the spatial distribution of the prey and not only to the fluctuation of turbulent water motions. Indeed, as proposed in the frame of optimal foraging theory (Pyke, 1984), zooplankton living in highly heterogeneous environments could reveal strategies devoted to exploiting high-density patches and then to optimize the energy required to capture a given amount of food. This could be achieved, as suggested in a few laboratory studies undertaken in non-turbulent conditions, (i) by increasing both the swimming speed and the complexity of swimming paths with increasing food density, and (ii) in accordance with area-restricted searching strategy, by decreasing the swimming speed or reducing motility in food patches (e.g. Tiselius, 1992; Bundy et al., 1993; van Duren and Videler, 1995). Consequently, in order to estimate an average encounter rate between

predator and prey, one needs first to consider very carefully the distributions of both the physical and biological variables we are dealing with, and second the potential effect of these distributions on the average encounter rate, and thus, on zooplankton behavior.

Herein, assuming statistical independence between turbulent kinetic energy dissipation rate and phytoplankton distribution, we derive simple equations from classical encounter theory in the multifractal frame that take into account both turbulence and behavior contributions to the encounter rates between predator and prey. Our conceptual approach is somewhat similar to that of Kiørboe and Saiz (1995), but our results are more general in that they provide for the very first time an objective way to examine direct and indirect effects of intermittent turbulence on predator–prey encounter rates. First, we evaluate the effect of turbulence on predator–prey encounter rates in an intermittent frame, and finally, we conceptually investigate the potential effects of zooplankton behavioral responses to the related small-scale phytoplankton patchiness.

## 2. Turbulence and encounter rates in plankton: model formulation

In the ocean, the encounter rate between planktonic predator and prey depends on the relative density and velocity of predator and prey. Moreover, the relative velocity between predator and prey has now been widely demonstrated to be a function of swimming behavior of both predator and prey and small-scale turbulent water motions (see e.g. Dower et al., 1997; Kiørboe, 1997, for a review). In particular, in order to evaluate for what types of predators turbulence is likely to be of importance, predator–prey encounter rate  $E$  (encounter  $s^{-1}$ ) can be written as (Kiørboe and Saiz, 1995)

$$E = E_{\text{behavior}} + E_{\text{turbulence}}, \quad (1)$$

where  $E_{\text{behavior}}$  and  $E_{\text{turbulence}}$  are the encounter rates due to the behavior of the organisms and to turbulent water motions. Considering that both predator and prey swim along straight lines in random directions, the behavioral encounter rate  $E_{\text{behavior}}$  is defined as (Gerritsen and Strickler, 1977)

$$E_{\text{behaviour}} = C\pi R^2 \left( \frac{u^2 + 3v^2}{3v} \right), \quad (2)$$

where  $C$  is the number of prey per unit volume (prey  $m^{-3}$ ),  $R$  is the perceptive distance of the predator (m), and  $u$  ( $m s^{-1}$ ) and  $v$  ( $m s^{-1}$ ), are the velocity of prey and predator, respectively. Assuming that  $u = 0$  for phytoplankton cells, Eq. (2) can be simplified as

$$E_{\text{behaviour}} = C\pi R^2 v. \quad (3)$$

On the other hand, the encounter rate due to turbulence is expressed following Rothschild and Osborn (1988) as

$$E_{\text{turbulence}} = C\pi d^2 w, \quad (4)$$

where  $w$  ( $m s^{-1}$ ) is the characteristic turbulent velocity enhancing the relative motion between predator and prey. According to Kolmogorov (1941) (see also Monin and Yaglom, 1975), for relative motion at a scale  $d$  is  $w^2 = C\varepsilon^{2/3}d^{2/3}$ , where  $C$  is a constant and  $\varepsilon$  is the small-scale

turbulent dissipation rate belonging to the inertial range. In the frame of predator–prey interactions,  $w$  can then be written as (Rothschild and Osborn, 1988)

$$w = 1.9(\varepsilon d)^{1/3}. \quad (5)$$

When the encounter takes place, the separation distance between predator and prey is also the perceptive distance of the predator, i.e.  $d = R$  (Denman and Gargett, 1995; Kiørboe and Saiz, 1995; Kiørboe and MacKenzie, 1995; MacKenzie and Kiørboe, 1995; Visser and MacKenzie, 1998). Because water motion differs below and above the Kolmogorov length scale  $l_k$  — the scale where viscous effects start to smooth out turbulent fluctuations and cannot be neglected ( $l_k = (\nu^3/\varepsilon)^{0.25}$  where  $\nu$  is the kinematic viscosity, ca.  $10^{-6} \text{ m}^2 \text{ s}^{-1}$ ) — the equations relating turbulent velocity  $w$  and  $\varepsilon$  are different, and the encounter rates due to turbulence also differ. The rms velocity  $w$  should then be expressed as  $w = 1.37(\varepsilon R)^{1/3}$  for  $R > l_k$  (Delichatsios and Probst, 1975), and  $w = 0.42R(\varepsilon/\nu)^{1/2}$  for  $R < l_k$  (Jackson and Lochman, 1993), where  $(\varepsilon/\nu)^{1/2}$  is the sub-Kolmogorov scale shear fluid rate ( $\gamma, \text{ s}^{-1}$ ). In intermittent turbulence, this distinction is, however, not as sharp as it may appear at first glance, and the Kolmogorov length scale ceases to be a reference frame (Frisch, 1995). Moreover, Hill et al. (1992) have demonstrated that Eq. (5) is valid well below the Kolmogorov length scale. Thus in the following, we will consider that application of Eq. (5) is warranted at the spatial scales relevant to planktivorous predators such as copepods. Finally, inserting the expression for the rms turbulent velocity  $w$  [Eq. (5)] in Eq. (4) yields

$$E_{\text{turbulence}} = 1.9C\pi R^{7/3}\varepsilon^{1/3}. \quad (6)$$

Following the seminal work of Rothschild and Osborn (1988), different expressions of the previous equations that yield slightly different results have been widely applied to both copepods and fish larvae (e.g. Sundby and Fossum, 1990; MacKenzie and Leggett, 1991; Saiz, 1994; Kiørboe and Saiz, 1995; Kiørboe and MacKenzie, 1995; Caparroy and Carlotti, 1996). All these approaches implicitly assumed that both zooplanktonic or phytoplanktonic prey are randomly — with random we mean independent random variables expressing a lack of correlation between successive fluctuations — distributed in space and time, and we are not aware of any theoretical or empirical attempt to deal simultaneously with the potential effects of microscale turbulence intermittency and the associated phytoplankton patchiness on encounter rates in plankton. This is, however, now feasible following the recent advent of multifractal concepts in marine ecology (Pascual et al., 1995; Seuront et al., 1996a, b; 1999).

### 3. Intermittency and multifractal formalism

A new field of marine research has recently been proposed, with the introduction of multifractals, for the analysis and modeling of marine intermittency (Pascual et al., 1995; Seuront et al., 1996a, b; 1999). The analysis of high-resolution time series of temperature, salinity and in vivo fluorescence recorded in the Eastern English Channel and the Southern Bight of the North Sea, showed that these fields are not homogeneous, but rather present bursts of activity at all scales, also called intermittent fluctuations, with skewed distributions far from Gaussian. These fluctuations have been analyzed in the multifractal framework, with statistical tools that are more general than standard methods (such as spectral analysis), which provide only limited information on the

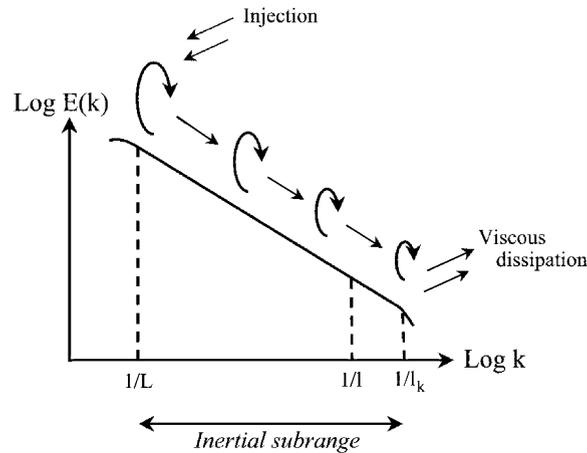


Fig. 1. Schematic representation showing the form of the energy spectrum of turbulent velocity cascade, where  $E(k)$  is the spectral density and  $k$  is a wave number ( $\text{m}^{-1}$ ). The kinetic energy generated at large-scale  $L$  cascades through the inertial subrange, i.e. a hierarchy of eddies of decreasing size to the viscous Kolmogorov scale  $l_k$ , where it is dissipated into heat. Practically, this cascade is observed between the outer scale  $L$ , and the resolution scale,  $l$ , of the measurements (often limited by the size of the sampling apparatus), leading to the scale ratio  $\lambda = L/l$ .

statistics of the process. Thus, whereas random variability has been often modeled in marine ecology in the Gaussian framework, e.g. Gaussian distributions and Brownian motion (Visser, 1997; Yamazaki and Okubo, 1995), here, we will generalize this approach to fully take into account the intermittency of turbulent processes and phytoplankton distribution. In the present paper, we will only review the main properties of a multifractal field (for more details on the use of multifractal algorithms to marine ecology studies, the interested reader can refer to Seuront et al., 1999). In a more general frame, a recent review paper by Shraiman and Siggia (2000) also provides some salient information about the structure of scalar fields advected by turbulent flows.

The intermittency of a multifractal field is such that its fluctuations are not destroyed by smoothing at any scale, until the outer scale of the system is reached. This means that a multifractal field  $Q$  averaged over a scale  $l$  will have a scale-dependent value denoted as  $Q_l$ , or in a more general way as  $Q_\lambda$ , where we introduce a non-dimensional scale ratio  $\lambda$  ( $\lambda = L/l$ ) as the ratio between the larger outer scale  $L$  and the resolution scale  $l$  of the measurements belonging to the inertial subrange, i.e.  $L \leq l \leq l_k$  (Fig. 1). The scale ratio can reach high values, so we assume in the following that  $\lambda \gg 1$ . The scale-dependent multifractal field  $Q_\lambda$  can be described by its probability distribution, or equivalently, by its statistical moments  $\langle (Q_\lambda^q) \rangle$ , where we consider any  $q \geq 0$ . For a multifractal field these moments scale with the ratio  $\lambda$  as (Schertzer and Lovejoy, 1987)

$$\langle (Q_\lambda)^q \rangle = Q_0^q \lambda^{K(q)}, \quad (7)$$

where ' $\langle \cdot \rangle$ ' indicates statistical or spatial averaging,  $Q_0 = \langle Q_\lambda \rangle$  is the mean of the multifractal process  $Q_\lambda$ , and  $K(q)$  is a scale-invariant moment function which is convex and satisfies  $K(0) = 0$  and  $K(1) = 0$ . Knowledge of  $K(q)$  fully describes the statistics of the process in a manner equivalent to 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  $q \geq 0$ . We underline here

that Eq. (7) is valid only for scales belonging to the inertial subrange, thus for  $1 \leq \lambda \leq A$ , where  $A = L/l_k$  is the maximum scale ratio, between the larger outer scale  $L$  and the Kolmogorov scale  $l_k$  (i.e. the scale where viscous effects start to smooth out turbulent fluctuations and cannot be neglected).

Finally, Eq. (7) can be used to evaluate the average of a polynomial function  $f(Q_\lambda)$  of the multifractal field ( $Q_\lambda$ ):

$$f(Q_\lambda) = \sum_{p=0}^N a_p (Q_\lambda)^p, \quad (8)$$

where  $a_p$  are constants, and  $p$  the polynomial order of the function  $f(Q_\lambda)$ . Then, using Eq. (7), averaging the function  $f(Q_\lambda)$  gives

$$\langle f(Q_\lambda) \rangle = \sum_{p=0}^N a_p Q_0^p \lambda^{K(p)}. \quad (9)$$

This general equation will be widely used in the following.

#### 4. Significance of intermittency for encounter rates

To evaluate the potential significance of intermittency for predator–prey encounter rates we need to compare the encounter rates expected in the case of homogeneous and intermittent (i.e. multifractal) turbulence and phytoplankton fields, i.e. introducing the precise statistical distributions of turbulent dissipation rates and phytoplankton biomass in predator–prey equations defined above, instead of their average values. In the following we shall apply the concepts related to the statistical properties of intermittently distributed turbulent kinetic energy dissipation rate and phytoplankton biomass to the encounter rates due to turbulence and behavior.

##### 4.1. Effect of turbulence intermittency

Let the phytoplankton cell concentration  $C$  and the turbulent kinetic energy dissipation rate  $\varepsilon$  be multifractal variables characterized by the scaling moment functions  $K_C(q)$  and  $K_\varepsilon(q)$  defined above, and by their means  $\langle C_\lambda \rangle = C_0$  and  $\langle \varepsilon_\lambda \rangle = \varepsilon_0$ , respectively. Here,  $E_{\text{turbulence}}$  and  $E_{\text{behavior}}$  will be regarded as estimates of encounter rates due to turbulence and behavior under the hypothesis of homogeneous turbulence and prey distributions, i.e.  $E_{\text{turbulence}} = E(C_0, \varepsilon_0)$  and  $E_{\text{behavior}} = E(C_0)$ . On the other hand,  $E'_{\text{turbulence}}$  and  $E'_{\text{behavior}}$  will estimate encounter rates due to turbulence and behavior when  $C_\lambda$  and  $\varepsilon_\lambda$  are regarded as multifractal variables, i.e.  $E'_{\text{turbulence}} = E(C_\lambda, \varepsilon_\lambda)$  and  $E'_{\text{behavior}} = E(C_\lambda)$ . The scale ratio  $\lambda$ , introduced to describe the inertial subrange statistical behavior of a multifractal variable in Eqs. (7) and (9), will be denoted as  $\lambda_\varepsilon$  and  $\lambda_C$  for turbulence and phytoplankton distributions, respectively.

Under the general hypothesis of independence of the variables  $C_\lambda$  and  $\varepsilon_\lambda$ , which still remains to be tested in the ocean, Eq. (6) is rewritten as

$$E'_{\text{turbulence}} = \langle E(C_\lambda, \varepsilon_\lambda) \rangle = 1.9\pi R^{7/3} \langle C_\lambda \rangle \langle \varepsilon_\lambda^{1/3} \rangle \quad (10)$$

and then

$$E'_{\text{turbulence}} = \langle E(C_\lambda, \varepsilon_\lambda) \rangle = 1.9\pi R^{7/3} C_0 \varepsilon_0^{1/3} \lambda_\varepsilon^{K_\varepsilon(1/3)}. \quad (11)$$

In more practical terms, to compute Eq. (11) one needs mean values of turbulent kinetic energy dissipation rate  $\varepsilon_0$ , phytoplankton concentration  $C_0$ , and the scale ratio  $\lambda_\varepsilon$  of the inertial subrange (Fig. 1) associated with a given experiment. Now  $E(C_0, \varepsilon_0) = 1.9\pi R^{7/3} C_0 \varepsilon_0^{1/3}$  [ $E(C_\lambda, \varepsilon_\lambda) = E(C_0, \varepsilon_0) \lambda_\varepsilon^{K_\varepsilon(1/3)}$ ],  $\lambda_\varepsilon \gg 1$  and  $K_\varepsilon(\frac{1}{3}) < 0$ ; therefore

$$E'_{\text{turbulence}} < E_{\text{turbulence}}. \quad (12)$$

This suggests that using a mean value of the turbulent kinetic energy dissipation rate  $\varepsilon_0$  instead of the multifractal distribution  $\varepsilon_\lambda$  leads to an overestimate of the contribution of turbulence to the predator–prey encounter rate.

In order to quantify the negative effect of the intermittent nature of turbulent energy dissipation rates  $\varepsilon_\lambda$  on the encounter rate due to turbulence, we need to compare the relative magnitudes of  $E_{\text{turbulence}}$  and  $E'_{\text{turbulence}}$ . First, one needs to note that this effect depends on the scale ratio  $\lambda_\varepsilon$  of large and small turbulent scales. Nevertheless, the power  $K_\varepsilon(\frac{1}{3})$  acts as a moderator of this effect, since it is usually quite small, e.g.  $K_\varepsilon(\frac{1}{3}) = -0.05$ , as extrapolated from atmospheric turbulence (Schmitt et al., 1992a, b; 1993; 1994). Thus, with a scale ratio  $\lambda_\varepsilon = 1000$ , this would yield  $E'_{\text{turbulence}} = 0.70E_{\text{turbulence}}$ .

We then investigated this potential decrease in the encounter rate estimate by fully developed intermittent turbulence on the basis of both basic spectral estimates and instantaneous intermittent distributions of turbulent energy dissipation rates of grid generated turbulence. Microscale turbulence was generated by means of fixed PVC grids (diameter 2 mm, mesh size 1 cm) in a circular flume. Instantaneous horizontal turbulent velocity was measured by high frequency (100 Hz) hot-film velocimetry, and turbulent energy dissipation rate was subsequently estimated in several ways. The average turbulent energy dissipation rate was derived following Tennekes and Lumley (1972) from the turbulence spectrum obtained from Fourier analysis of time series data recorded by the hot-film probe

$$\varepsilon = 15\nu \int_0^\infty k^2 E(k) dk, \quad (13)$$

where  $\varepsilon$  is the turbulent dissipation rate ( $\text{m}^2 \text{s}^{-3}$ ),  $\nu$  the kinematic viscosity ( $\text{m}^2 \text{s}^{-1}$ ),  $k$  the wave number ( $k = 2\pi/\lambda$ ,  $\text{m}^{-1}$ ),  $\lambda$  the eddy wavelength (m), and  $E(k)$  the turbulence spectrum ( $\text{m s}^{-2}$ ). The spectrum  $E(k)$  can be thought of as the mean-square amplitude of velocity fluctuations associated with a wave number of turbulent motion; these turbulent motions are conveniently thought of as eddies of characteristic size corresponding to their wavelength.

In order to take into account the intermittent nature of turbulence, we now need to consider local values,  $\varepsilon_l$ , of the turbulent dissipation rate following the refined similarity hypothesis (Kolmogorov, 1962; Obukhov, 1962) as

$$\Delta v_l = C \varepsilon_l^{1/3} l^{1/3}, \quad (14)$$

where  $C$  is a constant nearly equal to 1 (Visser and MacKenzie, 1998), and  $\Delta v_l = |v(x+l) - v(x)|$  is the velocity shear at scale  $l$ . Instantaneous values of  $\varepsilon_l$  were then subsequently estimated at the

Table 1

Comparison between the turbulent energy dissipation rates estimated from power spectra ( $\varepsilon_0$ ) and from fractional differentiation of order  $\frac{1}{3}$  ( $\varepsilon_t$ ), and the related differences in the estimated predator–prey encounter rates due to turbulence estimated both directly from the 40 empirical time series [ $(E_\varepsilon - E_{\varepsilon_t})/E_\varepsilon$ ] using  $\varepsilon_0$  and  $\varepsilon_t$  values in Eq. (6), and from different values of the characteristic exponent ( $K_\varepsilon(\frac{1}{3})$ ) introduced in Eq. (11) [ $(E_{\text{turbulence}} - E'_{\text{turbulence}})/E_{\text{turbulence}}$ ]. Mean values and standard deviations of  $(E_\varepsilon - E_{\varepsilon_t})/E_\varepsilon$ ,  $K_\varepsilon(\frac{1}{3})$  and  $(E_{\text{turbulence}} - E'_{\text{turbulence}})/E_{\text{turbulence}}$  are given in italics

$v$ (cm s <sup>-1</sup> )	$\varepsilon_0$	$\varepsilon_t$ (SD)	$\varepsilon/\varepsilon_t$	$(E\varepsilon_0 - E\varepsilon_t)/E\varepsilon_0$	$K_\varepsilon(\frac{1}{3})$	$(E_{\text{turbulence}} - E'_{\text{turbulence}})/E_{\text{turbulence}}$	
10	9.12E-07	9.55E-07	(2.40E-07)	0.95	32.26	- 0.059	33.47
20	1.31E-06	1.26E-06	(3.12E-07)	1.04	36.52	- 0.061	34.39
30	2.01E-06	2.11E-06	(4.89E-07)	0.95	39.87	- 0.060	33.93
40	4.87E-06	4.79E-06	(1.38E-06)	1.02	35.59	- 0.063	35.29
50	8.08E-06	7.80E-06	(2.12E-06)	1.04	38.59	- 0.064	35.73
60	1.14E-05	9.62E-06	(2.49E-06)	1.05	33.48	- 0.058	33.01
70	1.40E-05	1.31E-05	(3.37E-06)	1.07	33.88	- 0.066	36.61
80	2.35E-05	2.28E-05	(6.12E-06)	1.03	36.59	- 0.064	35.73
90	7.50E-05	7.11E-05	(2.18E-05)	1.05	37.68	- 0.064	35.73
100	1.05E-04	9.28E-05	(2.45E-05)	1.08	38.12	- 0.065	36.17
				<i>36.26 (2.45)</i>		<i>- 0.063 (0.002)</i>	<i>35.32 (1.25)</i>

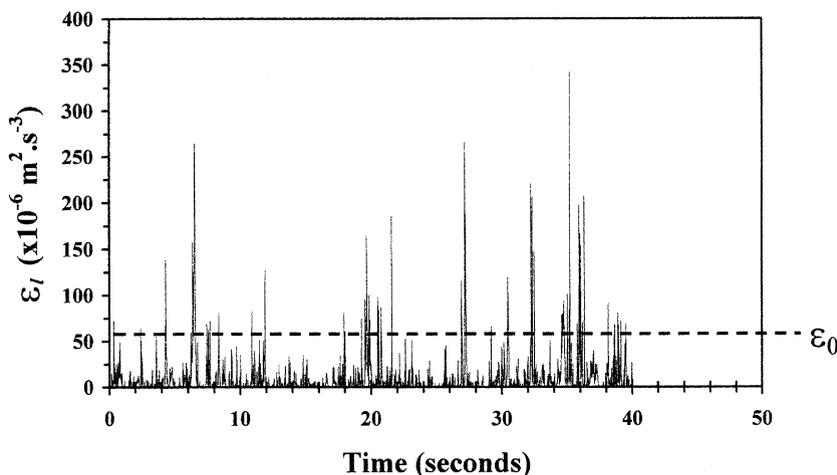


Fig. 2. Comparison between the instantaneous distributions of turbulent energy dissipation rates ( $\varepsilon_t$ ) estimated from fractional differentiation of order  $\frac{1}{3}$  and the mean value ( $\varepsilon_0$ ) estimated from power spectra.

smallest available resolution (i.e. 100 Hz) as a fractional differentiation of the local velocity shear  $\Delta v_t$ , raised to the third power (i.e.  $\varepsilon_t = (\Delta v_t/l^{1/3})^3$ ). Let us mention briefly that a fractional differentiation of order  $\frac{1}{3}$  corresponds to a multiplication by  $k^{1/3}$  in Fourier space equivalent to power law filtering (see Schertzer and Lovejoy, 1987; Schertzer et al., 1998). We then estimated both  $E_{\text{turbulence}}$  and  $E'_{\text{turbulence}}$  on the basis of 40 experiments conducted for mean velocity fields ranging from 10 to 100 cm s<sup>-1</sup> (Table 1). Thus, considering a mean value of the turbulent kinetic energy

dissipation rates ( $\varepsilon_0$ ) instead of the instantaneous values  $\varepsilon_t$  (Fig. 2) overestimates the encounter rates due to turbulence by about  $36.26 \pm 2.45\%$  (a value similar to the 30% estimated above) for values of the kinetic energy dissipation rate ranging from  $10^{-6}$  to  $10^{-4} \text{ m}^2 \text{ s}^{-3}$ ; values characterizing highly turbulent areas such as coastal and frontal areas (MacKenzie and Leggett, 1991). In order to generalize the previous results, we subsequently estimated the values of  $K_\varepsilon(\frac{1}{3})$  from our 40 time series dataset [ $K_\varepsilon(\frac{1}{3}) = -0.063 \pm 0.002$ ], and the associated difference between  $E_{\text{turbulence}}$  and  $E'_{\text{turbulence}}$  using  $K_\varepsilon(\frac{1}{3})$  and  $\lambda_\varepsilon = 1000$  in Eq. (12). We consistently found that  $E'_{\text{turbulence}} = \Phi E_{\text{turbulence}}$ , with  $\Phi = 64.68 \pm 1.25\%$ . Finally, one may note that the values of the exponent  $K_\varepsilon(\frac{1}{3})$  estimated from our laboratory experiment can be regarded as being realistic proxies of turbulent field conditions as far as they do not appear to be significantly different (Wilcoxon-Mann-Whitney  $U$ -test,  $p > 0.05$ ) from  $K_\varepsilon(\frac{1}{3})$  values estimated from high-resolution shear vertical profiles recorded in tidally mixed Japanese waters, i.e.  $K_\varepsilon(\frac{1}{3}) = -0.060 \pm 0.003$  (Seuront and Yamazaki, unpublished data). Furthermore, considering the similarity of the results obtained using atmospheric and oceanic turbulence data (i.e.  $E'_{\text{turbulence}} = 0.70E_{\text{turbulence}}$  and  $E'_{\text{turbulence}} = 0.65E_{\text{turbulence}}$ , respectively), these results suggest a strong similarity of intermittent structure in the atmosphere and the ocean. Whatever that may be, the resolution of this particular issue is beyond the scope of the present paper.

#### 4.2. Effect of small-scale intermittent phytoplankton distribution

Consider a situation with a planktonic predator searching for phytoplanktonic prey intermittently distributed in a multifractal frame. In this simple situation, following the parametrization described by Seuront et al. (1996a,b; 1999) a copepod will experience a very heterogeneous phytoplankton field exhibiting local concentrations reaching up to 5 times the average field value. Previous laboratory experiments — while conducted in non-turbulent conditions — have suggested some zooplankton have behavioral adaptations to food density or food patchiness, such as reduced motility in high food concentrations and in food patches, both for ciliates (e.g. Jonsson and Johansson, 1997) and copepods (e.g. Tiselius, 1992; Bundy et al., 1993; Saiz et al., 1993; Tiselius et al., 1993), but others indicated an increasing swimming speed with increasing food densities (Bundy et al., 1993; van Duren and Videler, 1995).

Here, we examined the relative importance of phytoplankton patchiness for the behavioral component of the predator-prey encounter rate defined by Eq. (3). Four types of behavioral adaptations are considered: (i) a constant swimming speed used to mimic the straight swimming behavior of cruising predators, (ii) a density-dependent swimming speed, (iii) a constant swimming speed with an increasing swimming path complexity with increasing food concentration, and (iv) both a density-dependent swimming speed and an increasing swimming path complexity with increasing food concentrations.

##### Case I: Constant swimming speed

As stated above, the phytoplankton distribution is regarded as a multifractal variable characterized by its mean density  $\langle C \rangle = C_0$ , and the scaling moment function  $K_C(q)$ . In this case, Eq. (3) is simply rewritten as

$$E'_{\text{behavior}} = \langle E(C_\lambda) \rangle = \pi R^2 v C_0 \lambda_{\mathcal{C}}^{K_C(1)} \quad (15)$$

now  $E(C_0) = \pi R^2 v C_0$ , and  $K_C(1) = 0$  as defined above; therefore

$$E'_{\text{behavior}} = E_{\text{behavior}}. \quad (16)$$

This clearly demonstrates that small-scale phytoplankton patchiness cannot have any effect on the behavioral predator–prey encounter rate if predators are regarded as ‘passive’ particles characterized only by their swimming velocity, unable to adapt their behavior to the ambient conditions. This is, however, all the more unlikely following the large amount of literature demonstrating the great chemo- and mechanoreception abilities of planktonic copepods (e.g. Buskey, 1984; Strickler, 1982, 1985; Paffenhöffer and Lewis, 1990; Yen and Fields, 1992; Bundy et al., 1998). We then consider a more likely hypothesis based on a differential swimming speed regarded as a function of food density.

#### Case 2: Density-dependent swimming speed

For simplicity, we will assume that the swimming speed of the predator,  $v$ , is a linear function of the phytoplankton density  $C$  following  $v = aC + b$ , where  $a$  and  $b$  are constants, with  $a > 0$  and  $b > 0$ . In heterogeneous phytoplankton distributions, the velocity of the predator is given by  $v_{\text{hetero}} = aC_\lambda + b$ , where  $C_\lambda$  is a multifractal variable characterized by the scaling moment functions  $K_C(q)$  previously defined (cf. Section 3), and by its mean  $\langle C_\lambda \rangle = C_0$ . In contrast, the constant predator velocity in homogeneous phytoplankton fields is simply defined with respect to the mean value  $C_0$  as  $v_{\text{homo}} = aC_0 + b$ . Thus, Eq. (15) yields (Eqs. (7), (8) and (9))

$$E'_{\text{behavior}} = \langle E(C_\lambda) \rangle = \pi R^2 (aC_0^2 \lambda C_0^{K_C(2)} + bC_0). \quad (17)$$

Considering  $E(C_0) = \pi R^2 (aC_0^2 + bC_0)$ , Eq. (17) yields

$$E'_{\text{behavior}} > E_{\text{behavior}}. \quad (18)$$

In this case, we find that such a simple behavioral adaptation to phytoplankton patchiness can have salient consequences on the behavioral encounter rate initially defined by Eq. (3). Thus, a positive effect could be expected when the swimming speed increases with increasing phytoplankton densities, which has been experimentally demonstrated on two copepod species, *Centropages velificatus* (Bundy et al., 1993) and *Temora longicornis* (van Duren and Videler, 1995) for phytoplankton concentrations within the range of cell densities found in waters where those species are abundant. Alternatively, a negative effect could be expected when the swimming speed decreases with increasing phytoplankton densities, i.e.  $a < 0$  (e.g. Buskey, 1984; Tiselius, 1992; van Duren and Videler, 1995). However, this particular situation has been observed only in a few laboratory experiments conducted on *Pseudocalanus minutus* in the presence of phytoplankton and in filtered seawater (Buskey, 1984), or on *Temora longicornis* at very high food concentrations (van Duren and Videler, 1995), both situations quite unrealistic in the frame of a potential response of copepods to food patchiness. This particular question has been addressed elsewhere by Tiselius (1992) in his behavioral study of *Acartia tonsa* in patchy food environments. However, his results demonstrated that the decreasing velocity in food patches is associated mainly with a global decrease in jump frequencies, which we did not take into account here as jumping behavior is not associated with an active feeding process, and a simultaneous increase of residence time in high food concentration areas (see Tiselius, 1992, his Fig. 7). The latter question will precisely be developed in the two next cases.

In any case, in the particular situation where  $a > 0$ , the effect of phytoplankton patchiness is here quite important. Indeed,  $K(2) = \mu$  is usually denoted as the intermittency parameter that has already been estimated as being in the range 0.1–0.3 for passive scalars — as phytoplankton cells are — distributed in turbulent flows (Prasad et al., 1988; Meneveau and Sreenivasan, 1991; Sreenivasan and Kailasnath, 1993; Seuront et al., 1996a, b; 1999). Scale ratios of  $\lambda_C = 100$  (Seuront et al., 1996a) and  $\lambda_C = 20$  (Seuront et al., 1999) thus, respectively, give enhancing factors of 1.6–6.3 and 1.4–3.3 of the encounter rate due to intermittent phytoplankton distributions. In the two previous empirical studies, phytoplankton cells have been shown to behave as a purely passive scalar over spatial scale ratios  $\lambda_C$  of 100 and 20. One may thus hypothesize that such a behavior could still be observed to the smallest scales (i.e. Batchelor scales), and a potential scale ratio of  $\lambda_C = 1000$  can be reasonably suggested for phytoplankton distribution in the ocean, leading to enhancing factors of the behavioral encounter rate defined in Eq. (18) in the range 2.0–8.0. Moreover, from this particular point of view, the effect of phytoplankton patchiness is more significant for cruising than for ambush feeding predators, and also for fast swimming predators (high  $v$ ).

One may also note that in the particular case where the predator swimming velocity is very slow, even nil, in the absence of food (i.e.  $b \cong 0$ ), then the speed of the predator would be close to zero when between high density food patches (or in areas lacking food). In this case, the total encounter rate over long periods of time would go to nearly zero, as the predator would be spending all of its time moving very slowly through regions devoid of food, and it could take a long time before the predator reached another region of high food density. Thus, the encounter outcome of a predator experiencing a homogeneous phytoplankton distribution might be higher. This effect would nevertheless be difficult to estimate because it is intrinsically dependent on three related processes, the spatial structure of phytoplankton distribution, the perceptive ability of a given predator to scan its surrounding environment, and the behavioral adaptation to the absence of food such as reduced motility (Tiselius, 1992; Saiz, 1994). Whatever that may be, in the particular case where  $b = 0$  encounter rate might not be so small, as passive sinking occurring in the absence of active swimming (Tiselius and Jonsson, 1990) could contribute first to increase the encounter rate between the “non-motile” predator and prey (Kiørboe and Saiz, 1995), and second to bring a predator into higher concentration food areas. Finally, we also need to be aware of the fact that a non-swimming predator can generate strong feeding currents (i.e. up to  $1 \text{ cm s}^{-1}$  for the copepod *Eucalanus crassus* (Strickler, 1982, 1985)) that contribute to moving prey relative to the predator, thus enhancing the predator–prey encounter rate (Kiørboe and Saiz, 1995; Osborn, 1996). The creation, as well as the intensification, of a feeding current can thus be regarded as being conceptually equivalent to a “swimming speed” in terms of encounter rates, leading to a more general meaning of Eqs. (3), (15) and (17).

### Case 3: Constant swimming speed and patch exploitation strategy

This hypothesis has been drawn following empirical results which demonstrate the ability of zooplanktonic organisms to detect and to remain in food patches. This could be achieved following different strategies such as an increase in the swimming path complexity (e.g. Bundy et al., 1993), but can be generally summed up considering that the time spent by a copepod in a food patch is all the more important when the associated food density is elevated.

So, let  $C_{\min}$  be the hypothetical minimal food patch density, in which case the time,  $t$ , spent in the considered patch is set to be unity (i.e.  $t = 1$ ). For a given food quantity  $C$ , such as  $C > C_{\min}$ , the

time spent in a food patch will be non-dimensionally expressed as  $t = C/C_{\min}$ . Finally, the biological encounter rate  $E'_{\text{behaviour}}$  is expressed as an addimensional expansion of Eq. (3) as

$$E'_{\text{behavior}} = \langle E(C_{\lambda}) \rangle = \frac{\pi R^2 v}{C_{\min}} C_0^2 \lambda_c^{K_c(2)} \quad (19)$$

now  $E(C_0) = (\pi R^2 v / C_{\min}) C_0$  and  $K_c(2) > 0$ , therefore

$$E'_{\text{behavior}} > E_{\text{behavior}}. \quad (20)$$

Thus, predators able to develop strategies to remain in a given high food density patch will substantially increase — up to a factor  $C_0^2 \lambda_c^{K_c(2)} / C_{\min}$  — their effective encounter rate with phytoplankton cells. Following the previously chosen formalism, this effect will be all the more important when the prey density is high (see Eq. (19)). Finally, this could be the most likely behavioral adaptation to resource patchiness, as this strategy has been found for a wide variety of organisms and prey patchiness (Coughlin et al., 1992; Larsson and Kleiven, 1996; Bascompte and Vila, 1997; Jonsson and Johansson, 1997; Kostylev et al., 1997; Ritchie, 1998).

#### Case 4: Density-dependent swimming speed and patch exploitation

Introducing the previous density-dependent swimming speed,  $v = aC + b$ , in Eq. (19) now yields

$$E'_{\text{behaviour}} = \langle E(C_{\lambda}) \rangle = \frac{\pi R^2}{C_{\min}} (aC_0^3 \lambda_c^{K_c(3)} + bC_0^2 \lambda_c^{K_c(2)}). \quad (21)$$

With  $E(C_0) = (\pi R^2 / C_{\min}) (aC_0^3 + bC_0^2)$ , and as previously stated when we tested the effect of a density-dependent swimming speed alone (i.e.  $a > 0$  and  $b \geq 0$ ), it becomes

$$E'_{\text{behavior}} > E_{\text{behavior}}. \quad (22)$$

This particular situation can be regarded as a generalization of Eq. (17) to a more complete and complex behavioral response to phytoplankton patchiness. In particular, for  $a > 0$ , we have Eq. (17) < Eq. (21), indicating an increased behavioral contribution to predator-prey encounter rates. Indeed, the scale ratio  $\lambda_c$  is usually quite large and  $K_c(3)$  is in the range 0.3–0.6 for passive scalars advected by fully turbulent flows (Schmitt et al., 1996; Seuront et al., 1996a, b; 1999), giving for  $\lambda_c = 100$  and  $\lambda_c = 20$  enhancing factors in the range 3.0–16 and 2.5–6.0, respectively. Here our test-case  $\lambda_c = 1000$  would lead to an enhancing factor in the range 8.0–63.0. As previously stated, a negative effect could a priori be expected when the swimming speed decreases within phytoplankton patches (i.e.  $a < 0$  and  $b \geq 0$ ). However, as pointed out in our test-case 2, a copepod getting inside a food patch stops searching (i.e. swimming) and starts filtering, generating a feeding current equivalent to a swimming velocity in Eqs. (3), (15), (17), (19) and (21) as far as it increases the relative velocity between predator and prey, and then the effective encounter rate. There is then no loss of generality in Eq. (21) shifting between swimming velocity and feeding current when the predator is located outside and inside food patches, respectively.

While further investigations could have been conducted in order to provide further insight into the analytical properties of the previous equations, the resolution of this particular issue is beyond the scope of this contribution. Let us nevertheless recall that, as demonstrated by Kiørboe and Saiz (1995) and Kiørboe and MacKenzie (1995), the swimming speed of planktonic predators is very dependent on their size, suggesting that the previously demonstrated effect of behavior will be all the more important when the predators are large (i.e. high  $v$  values in Eqs. (15) and (19), and high

$b$  values in Eqs. (17) and (21)). Moreover, Eqs. (15), (17), (19) and (21)) are also sensitive to the perceptible distance of the predator ( $R$ ), which is decreased in high hydrodynamic conditions (Kiørboe and Saiz, 1995), leading to an increase in the behavioral contribution to the predator–prey encounter rates in low hydrodynamic conditions. Moreover, these features could also provide an alternative explanation to the apparent inadequacy observed by Saiz (1994) between empirical encounter rates and the theoretical values expected following the basic particle encounter theory.

Thus, we propound that the theoretical framework provided in this paper could be of prime practical importance for marine ecologists dealing with grazing estimates both in the field and in the laboratory. Indeed, the fact that present studies of zooplankton trophodynamics resolve so little of the variance in feeding due to turbulence could be precisely associated with the fact that these studies might have been based on erroneous hypotheses, i.e. turbulence homogeneity and random prey distributions. Another factor could be that experimental turbulent setup was unsuitable for generating realistic turbulent conditions, e.g. in terms of inertial subrange (see e.g. Peters and Redondo, 1997, for more discussion on the subject), and thus failed to fit theoretical predictions. We therefore think that the first step to improve trophodynamics studies should be to make careful measurements of both turbulence and phytoplankton distributions (i.e. the exponents  $K_\varepsilon(\frac{1}{3})$  and  $K_C(2)$ , respectively), and the magnitude of the inertial subranges  $\lambda_\varepsilon$  and  $\lambda_C$  associated with turbulence and phytoplankton distributions, respectively. Indeed, as far as recent studies conducted in a tidally driven coastal ecosystem demonstrated that the degree of patchiness of phytoplankton populations can be a function of (i) phytoplankton concentration, (ii) phytoplankton species composition and (iii) turbulence intensity (Seuront, 1999), one really needs to be aware of the precise nature of phytoplankton distributions to infer the results of any kind of feeding experiments. In addition, precise descriptions of the predator behavior, as have been done both empirically (Strickler, 1998; Doal et al., 1998) and numerically (Jiang et al., 1999), should lead to improvements or more exact formulations of Eqs. (15), (17), (19) and (21).

## 5. Conclusions

The general result here is first that the effect of turbulence on predator–prey encounter rates is less important than previously thought on the basis of the hypothesis of homogeneous turbulence. Nevertheless, a numerical estimate of this effect in a test-case with  $\lambda_\varepsilon = 1000$  leads to a moderate effect of intermittency, due to the small value of the exponent  $K_\varepsilon(\frac{1}{3})$ . Afterwards, the contribution of behavioral components is obviously more important than when phytoplankton prey are regarded as being homogeneously distributed. An increase in encounter rates should not be regarded as a simple direct consequence of an increase in the relative velocity of the predator and the prey induced by turbulent velocity, but rather as both a direct and indirect consequence of intermittent microscale turbulence which generates heterogeneous phytoplankton distributions. Indeed, the scale ratio of the turbulent cascades (cf. Fig. 1) is of salient importance. With a test-case of  $\lambda_C = 1000$ , an intermittent (i.e. multifractal) phytoplankton distribution can thus enhance the behavioral component of the predator–prey encounter rate by a factor of up to 60 in our last case study, where the enhancing factor was dependent on the scale ratio  $\lambda_C$ .

The approach developed here was done with copepods in mind, but the equations can be easily applied to other planktivorous predators as well. Indeed, copepod distributions are also highly

heterogeneous (Tsuda, 1995), such that similar approaches could be conducted on the effects of both turbulence and intermittent copepod distributions on larval fish feeding behavior. This also suggests reconsidering the effects of microscale turbulence on estimates of plankton food requirements, and energy gain-and-loss for foraging. Indeed, following studies related to optimal foraging theory (Pyke, 1984), zooplankton living in highly heterogeneous environments could develop strategies to exploit high-density patches and then to optimize the energy required to capture a given amount of food. This could be achieved, as previously suggested, by increasing the complexity of swimming paths with increasing food densities, or reducing motility in food patches (Timbergen et al., 1967). Recent papers (Marguerit et al., 1998) dealing with grazing in heterogeneous (i.e. multifractal) phytoplankton fields have thus demonstrated that very simple behavioral strategies related to food quantity perceived by a predator could lead to different results in terms of swimming behavior and ingestion rates in comparison with what would have been obtained in homogeneous environments. A precise description of the behavior of both predators and prey then appears to be a salient issue for the future modeling of plankton trophodynamics in turbulent environments (Browman and Skiftesvik, 1996; Osborn and Scotti, 1996), propounding the advantage of individual-based approaches (Yamazaki, 1993; Levin, 1994; Seuront, 1999).

In reviewing the available literature on turbulence and larval fish feeding, Dower et al. (1997) pointed out that future research would do well to include non-homogenous prey distributions and predator behaviors that more realistically mimic field conditions. Indeed, in the field, patchiness is present at both temporal and spatial scales. Systematic studies of simplified mimics and real plankton organisms of widely varying nature and behavioral properties in a diversity of steady and unsteady flows are then still needed to dissect the multiple adaptative strategies of real organism in a real ocean. In that way, both the analytical model and the multifractal frame (see Seuront et al., 1999, for a review) may be a starting point to investigate the precise effects of the real nature of the surrounding physical and biological environments on both plankton behaviors and distributions.

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## **References**

- Bascompte, J., Vila, C., 1997. Fractals and search paths in mammals. *Landscape Ecology* 12, 213–221.
- Browman, H.I., Skiftesvik, A.B., 1996. Effects of turbulence on the predation cycle of fish larvae: comments on some of the issues. *Marine Ecology Progress Series* 139, 309–312.
- Bundy, M.H., Gross, T.F., Coughlin, D.J., Strickler, J.R., 1993. Quantifying copepod searching efficiency using swimming pattern and perceptive ability. *Bulletin of Marine Science* 53, 15–28.
- Bundy, M.H., Gross, T.F., Vanderploeg, H.A., Strickler, J.R., 1998. Perception of inert particles by calanoid copepods: behavioral observations and a numerical model. *Journal of Plankton Research* 20, 2129–2152.
- Buskey, E.J., 1984. Swimming patterns as an indicator of copepod sensory system in the recognition of food. *Marine Biology* 79, 165–175.

- Caparroy, P., Carlotti, F., 1996. A model for *Acartia tonsa*: effect of turbulence and consequences for the related physiological processes. *Journal of Plankton Research* 18, 2139–2177.
- Coughlin, D.J., Strickler, J.R., Sanderson, B., 1992. Swimming and search behaviour in clownfish, *Amphiprion perideraion*, larvae. *Animal Behaviour* 44, 427–440.
- Davis, C.S., Flierl, G.R., Wiebe, P.H., Franks, P.J.S., 1991. Micropatchiness turbulence and recruitment in plankton. *Journal of Marine Research* 49, 109–151.
- Denman, K.L., Gargett, A.E., 1995. Biological–physical interactions in the upper ocean: the role of vertical and small scale transport processes. *Annual Review of Fluid Mechanics* 27, 225–255.
- Delichatsios, M.A., Probst, R.F., 1975. Coagulation in turbulent flow: theory and experiment. *Journal of Colloid and Interface Science* 51, 394–405.
- Doal, M.H., Colin, S.P., Yen, J., Strickler, J.R., 1998. Locating a mate in 3D: the case of *Temora longicornis*. *Philosophical Transactions of the Royal Society of London B* 353, 681–690.
- Dower, J.F., Miller, T.J., Leggett, W.C., 1997. The role of microscale turbulence in the feeding ecology of larval fish. *Advances in Marine Biology* 31, 169–220.
- Frisch, U., 1995. *Turbulence*. Cambridge University Press, Cambridge.
- Gargett, A.E., 1997. “Theories” and techniques for observing turbulence in the euphotic zone. *Scientia Marina* 61, 25–45.
- Gerritsen, J., Strickler, J.R., 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. *Journal of Fish Research Board Canada* 34, 73–82.
- Hill, P.S., Nowell, A.R.M., Jumars, P.A., 1992. Encounter rate by turbulent shear of particles similar in diameter to the Kolmogorov scale. *Journal of Marine Research* 50, 643–668.
- Jackson, G.A., Lochmann, S., 1993. Modeling coagulation of algae in marine ecosystems. In: Buffle, J., van Leeuwen, H.P. (Eds.), *Environmental Analytical and Physical Chemistry Series, Vol. 2. Environmental Particles*. Lewis Publishers, Boca Raton, pp. 387–414.
- Jiang, H., Meneveau, C., Osborn, T.R., 1999. Numerical study of the feeding current around a copepod. *Journal of Plankton Research* 21, 1391–1421.
- Jimenez, J., 1997. Oceanic turbulence at millimeter scales. *Scientia Marina* 61, 47–56.
- Jonsson, P.R., Johansson, M., 1997. Swimming behaviour, patch exploitation and dispersal capacity of a marine benthic ciliate in flume flow. *Journal of Experimental Marine Biology and Ecology* 215, 135–153.
- Jou, D., 1997. Intermittent turbulence: a short introduction. *Scientia Marina* 61, 57–62.
- Kjørboe, T., 1997. Small-scale turbulence, marine snow formation, and planktivorous feeding. *Scientia Marina* 61, 141–158.
- Kjørboe, T., Saiz, E., 1995. Planktivorous feeding in calm and turbulent environments, with emphasis on copepods. *Marine Ecology Progress Series* 122, 135–145.
- Kjørboe, T., MacKenzie, B.R., 1995. Turbulence-enhanced prey encounter rates in larval fish: effects of spatial scale, larval behaviour and size. *Journal of Plankton Research* 17, 2319–2331.
- Kolmogorov, A.N., 1941. The local structure of turbulence in incompressible viscous fluid for very large Reynolds numbers. *Dokla Akademii Nauk SSSR* 30, 299–303.
- Kolmogorov, A.N., 1962. A refinement of previous hypotheses concerning the local structure of turbulence in viscous incompressible fluid at high Reynolds number. *Journal of Fluid Mechanics* 13, 82.
- Kostylev, V., Erlandson, J., Johannesson, K., 1997. Microdistribution of the polymorphic snail *Littorina saxatilis* (Olivi) in a patchy rocky shore habitat. *Ophelia* 47, 1–12.
- Larsson, P., Kleiven, O.T., 1996. Food search and swimming speed in *Daphnia*. In: Lenz, P.H., Hartline, D.K., Purcell, J.E., Macmillan, D.L. (Eds.), *Zooplankton: Sensory Ecology and Physiology*. Gordon & Breach, Amsterdam, pp. 375–387.
- Levin, S.A., 1994. Patchiness in marine and terrestrial systems: from individuals to populations. *Philosophical Transactions of the Royal Society of London B* 343, 99–103.
- MacKenzie, B.R., Kjørboe, T., 1995. Encounter rates and swimming behavior of pause-travel and cruise larval fish predator in calm and turbulent laboratory experiments. *Limnology and Oceanography* 40, 1278–1289.
- MacKenzie, B.R., Leggett, W.C., 1991. Quantifying the contribution of small-scale turbulence to the encounter rates between larval fish and their zooplankton prey: effects of wind and tide. *Marine Ecology Progress Series* 73, 149–160.
- MacKenzie, B.R., Miller, T.J., Cyr, S., Leggett, W.C., 1994. Evidence of a dome-shaped relationship between turbulence and larval fish ingestion rates. *Limnology and Oceanography* 39, 1790–1799.

- Marguerit, C., Schertzer, D., Schmitt, F., Lovejoy, S., 1998. Copepod diffusion within multifractal phytoplankton fields. *Journal of Marine Systems* 16, 69–83.
- Meneveau, C., Sreenivasan, K.R., 1991. The multifractal nature of turbulent energy dissipation. *Journal of Fluid Mechanics* 224, 429–484.
- Monin, A.S., Yaglom, A.M., 1975. *Statistical Fluid Mechanics: Mechanics of Turbulence*. MIT Press, London.
- Obukhov, A.M., 1962. Some specific features of atmospheric turbulence. *Journal of Fluid Mechanics* 13, 77.
- Osborn, T.R., 1996. The role of turbulent diffusion for copepods with feeding currents. *Journal of Plankton Research* 18, 185–195.
- Osborn, T.R., Scotti, A., 1996. Effects of turbulence on predator-prey contact rates: where do we go from here? *Marine Ecology Progress Series* 139, 302–304.
- Paffenhöffer, G.A., Lewis, K.D., 1990. Perceptive performance and feeding behavior of calanoid copepods. *Journal of Plankton Research* 12, 933–946.
- Pascual, M., Ascoti, F.A., Caswell, H., 1995. Intermittency in the plankton: a multifractal analysis of zooplankton biomass variability. *Journal of Plankton Research* 17, 1209–1232.
- Peters, F., Redondo, J.M., 1997. Turbulence generation and measurements: application to studies in plankton. *Scientia Marine* 61, 205–228.
- Prasad, R.R., Meneveau, C., Sreenivasan, K.R., 1988. The multifractal nature of the dissipation field of passive scalars in fully turbulent flows. *Physics Review Letters* 61, 74–77.
- Pyke, J.H., 1984. Optimal foraging theory: a critical review. *Annual Review Ecological Systems* 15, 523–575.
- Ritchie, M.E., 1998. Scale-dependent foraging and patch choice in fractal environments. *Evolution and Ecology* 12, 309–330.
- Rothschild, B.J., Osborn, T.R., 1988. Small-scale turbulence and plankton contact rates. *Journal of Plankton Research* 10, 465–474.
- Saiz, E., 1994. Observations of the free-swimming behavior of *Acartia tonsa*: effects of food concentration and turbulent water motion. *Limnology and Oceanography* 39, 1566–1578.
- Saiz, E., Tiselius, P., Jonsson, P.R., Verity, P., Paffenhöffer, G.A., 1993. Experimental records of the effects of food patchiness and predation on egg production of *Acartia tonsa*. *Limnology and Oceanography* 38, 280–289.
- Sanford, L.P., 1997. Turbulent mixing in experimental ecosystem studies. *Marine Ecology Progress Series* 161, 265–293.
- Schertzer, D., Lovejoy, S., 1987. Physically based rain and cloud modeling by anisotropic multiplicative turbulent cascades. *Journal of Geophysical Research* 92, 9693–9714.
- Schertzer, D., Lovejoy, S., Schmitt, F., Chigirinskaya, Y., Marsan, D., 1998. Multifractal cascade dynamics and turbulent intermittency. *Fractals* 5, 427–471.
- Schmitt, F., Lavallée, D., Schertzer, D., Lovejoy, S., 1992a. Empirical determination of universal multifractal exponents in turbulent velocity fields. *Physics Review Letters* 68, 305–308.
- Schmitt, F., Lavallée, D., Lovejoy, S., Schertzer, D., Hooge, C., 1992b. Estimations directes des indices de multifractals universels dans le champ de vent et de température. *Comptes Rendus de l'Académie des Sciences de Paris Série II* 314, 749–754.
- Schmitt, F., Schertzer, D., Lovejoy, S., Brunet, Y., 1993. Estimation of universal multifractal indices for atmospheric turbulent velocity fields. *Fractals* 1, 568–575.
- Schmitt, F., Schertzer, D., Lovejoy, S., Brunet, Y., 1994. Empirical study of multifractal phase transition in atmospheric turbulence. *Nonlinear Processes in Geophysics* 1, 95–104.
- Schmitt, F., Schertzer, D., Lovejoy, S., Brunet, Y., 1996. Multifractal temperature and flux of temperature in fully developed turbulence. *Europhysics Letters* 34, 195–200.
- Seuront, L., 1999. Hétérogénéité spatio-temporelle et couplage physique-biologie en écologie pélagique: implications sur les flux de carbone. PhD Thesis, Université des Sciences et Technologies de Lille, France.
- Seuront, L., Schmitt, F., Lagadeuc, Y., Schertzer, D., Lovejoy, S., Frontier, S., 1996a. Multifractal analysis of phytoplankton biomass and temperature in the ocean. *Geophysical Research Letters* 23, 3591–3594.
- Seuront, L., Schmitt, F., Schertzer, D., Lagadeuc, Y., Lovejoy, S., 1996b. Multifractal intermittency of Eulerian and Lagrangian turbulence of ocean temperature and plankton fields. *Nonlinear Processes in Geophysics* 3, 236–246.
- Seuront, L., Schmitt, F., Lagadeuc, Y., Schertzer, D., Lovejoy, S., 1999. Universal multifractal analysis as a tool to characterize multiscale intermittent patterns: example of phytoplankton distribution in turbulent coastal waters. *Journal of Plankton Research* 21, 877–922.

- Shraiman, B.I., Siggia, E.D., 2000. Scalar turbulence. *Nature* 405, 639–646.
- Sreenivasan, K.R., Kailasnath, P., 1993. An update of the intermittency exponent in turbulence. *Physical Fluids A* 5, 512–515.
- Strickler, J.R., 1982. Calanoid copepods, feeding currents and the role of gravity. *Science* 218, 158–160.
- Strickler, J.R., 1985. Feeding currents in calanoid copepods: two new hypothesis. *Symposium of the Society of Experimental Biology* 89, 459–485.
- Strickler, J.R., 1998. Observing free-swimming copepods mating. *Philosophical Transactions of the Royal Society of London B* 353, 671–680.
- Sundby, S., Fossum, P., 1990. Feeding conditions of Arcto-Norwegian cod larvae compared with the Rothschild–Osborn theory on small-scale turbulence and plankton contact rates. *Journal of Plankton Research* 12, 1153–1162.
- Tennekes, H., Lumley, J.L., 1972. *A First Course in Turbulence*. MIT Press, Cambridge, MA.
- Timbergen, N., Impekoven, M., Frank, D., 1967. An experiment on spacing-out as a defence against predation. *Behaviour* 28, 307–321.
- Tiselius, P., 1992. Behavior of *Acartia tonsa* in patchy food environments. *Limnology and Oceanography* 37, 1640–1651.
- Tiselius, P., Jonsson, P.R., 1990. Foraging behavior of six calanoid copepods: observations and hydrodynamic analysis. *Marine Ecology Progress Series* 66, 23–33.
- Tiselius, P., Jonsson, P.R., Verity, P.G., 1993. A model evaluation of the impact of food patchiness on foraging strategy and predation risk in zooplankton. *Bulletin of Marine Science* 53, 247–264.
- Tsuda, A., 1995. Fractal distribution of the oceanic copepod *Neocalanus cristatus* in the subarctic Pacific. *Journal of Oceanography* 51, 216–266.
- van Duren, L.A., Videler, J.J., 1995. Swimming behaviour of development stages of the calanoid copepod *Temora longicornis* at different food concentrations. *Marine Ecology Progress Series* 126, 153–161.
- Visser, A.W., 1997. Using random walks models to simulate the vertical distribution of particles in a turbulent water column. *Marine Ecology Progress Series* 158, 275–281.
- Visser, A.W., MacKenzie, B.R., 1998. Turbulence-induced contact rates of plankton: the question of scale. *Marine Ecology Progress Series* 166, 307–310.
- Yamazaki, H., 1993. Lagrangian study of planktonic organisms: perspectives. *Bulletin of Marine Science* 53, 265–278.
- Yamazaki, H., Okubo, A., 1995. A simulation of grouping: an aggregative random walk. *Ecological Modeling* 79, 159–165.
- Yen, J., Fields, D.M., 1992. Escape response of *Acartia hudsonica* (Copepoda) nauplii from the flow field of *Temora longicornis* (Copepoda). *Archiv Hydrobiol Beith Ergebn Limnology* 36, 123–134.