

NOTE

**Turbulence-induced contact rates of plankton:
the question of scale**

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ABSTRACT: Modelling encounter rates between planktonic predators and prey in turbulent waters requires an estimate of a spatial scale. One spatial scale proposed in the literature based on prey concentration is shown to be systematically inconsistent and its use is shown to imply that plankton sampling methodology can bias encounter rate estimates in turbulent situations. We show that a scale based on the predator's reactive distance is more appropriate, as it has clear theoretical support, and is consistent with other mathematical treatments of encounter problems. Applying the reactive distance as the length scale produces encounter rates for small (e.g. 4 to 10 mm) fish larvae 2- to 3-fold lower than those using prey separation distance.

KEY WORDS: Turbulence · Plankton · Predation · Encounter rate · Turbulent velocity scale · Spatial scale

An expression, first introduced by Rothschild & Osborn (1988) and modified by Evans (1989), describes the encounter rate, Z , of planktonic predators and their prey under turbulent conditions as

$$Z = c\pi R^2(u^2 + v^2 + 2w^2)^{1/2} \quad (1)$$

Here, c and u are the concentration and randomly directed behavioural motion of prey particles, R and v are the reactive distance and swimming velocity of the predator, and w is the root-mean-square turbulent velocity. This expression is purely mechanistic and describes the rate at which uniformly distributed, randomly moving particles enter a translating spherical volume of radius R in the presence of turbulence. Under this idealised representation, a particle entering the spherical volume constitutes an encounter, that is, a potential capture. The specific geometry of the perception volume can be more complicated than a simple sphere (e.g. Dower et al. 1997), and the probability of an encounter leading to successful capture and ingestion

is likely to be as much a function of biological as of physical factors (see details in, for example, Matsu-shita 1991, Jenkinson 1995, Kiørboe & MacKenzie 1995, Shimeta et al. 1995). This notwithstanding, Eq. (1) encapsulates a process which is a necessary precursor to any capture and ingestion event.

It is well known that w , the root-mean-square turbulent velocity, is scale dependent. That is, the relative velocity of 2 fluid elements becomes increasingly correlated as d , the distance between them, decreases. In particular, for d greater than the Kolmogorov scale, this has led to the formulation

$$w = \alpha(\epsilon d)^{1/3} \quad (2)$$

where α is a constant of order unity [Rothschild & Osborn (1988) give $\alpha = 1.9$ whereas Delichatsios & Probst (1975) find $\alpha = 1.37$] and ϵ is the turbulent dissipation rate.

A question that has been central to the empirical application of this theory is: What is the appropriate length scale, d , which should be used to estimate the turbulent encounter rate? Several earlier studies used the inter-prey separation distance (e.g. Sundby & Fossum 1990, MacKenzie & Leggett 1991, Kiørboe 1993, MacKenzie et al. 1994) whereas others have assumed that d is equal to either the dimension of the smallest turbulent eddies (Muelbert et al. 1994) or the 'eddy separation distance' (Davis et al. 1991). As a better understanding of the processes developed, it became more common to set $d = R$, the reactive radius of the predator (e.g. Evans 1989, Hill et al. 1992, Denman & Gargett 1995, Kiørboe & MacKenzie 1995, Osborn 1996, Yamazaki 1996). In most cases, the reasons for particular choices of scales have not been described in detail, leading to some confusion in the literature; it is this confusion that we wish to address here.

Recently, the reactive distance scaling has been strongly criticised in an unrefereed comment by Sund-

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by (1996), in favour of the inter-particle separation distance (Sundby 1997). Sundby (1996, 1997) maintains that the appropriate length scale is the mean inter-prey separation, $d = c^{-1/3}$. Sundby's rationale for this is that at a prey concentration of c , the mean separation of a predator to its prey is of the order $c^{-1/3}$ (specifically, for a Poisson distribution, the mean separation is $0.55c^{-1/3}$). At this distance, the turbulent velocity scale is $w = \alpha(\epsilon c^{-1/3})^{1/3}$ and it is velocities of this scale that can decrease the predator-prey separation. Up to this point Sundby's reasoning is correct and would remain correct if the turbulent velocity scale remained $w(r) = \alpha(\epsilon c^{-1/3})^{1/3}$ for all separation scales r lying between the inter-particle separation, $c^{-1/3}$, and the predator's reactive distance R . However, a reduction of the predator-prey separation at distance $c^{-1/3}$ does not constitute an encounter. An encounter only happens when $r \leq R$. As r approaches R , the uncorrelated component of the turbulent velocity fluctuations, i.e. that contributing to w , becomes less. That is, the rate at which turbulence can narrow the gap becomes slower. The critical value is reached at the reactive distance R . This is where turbulence can actually cause an encounter by bringing a prey item into the predator's perception volume. A salient point to note is that there is only a *possibility* that turbulence can reduce the predator-prey separation; it can just as likely *increase* the predator-prey separation.

In the simplest case, for a non-swimming predator feeding on passive prey, the encounter rate becomes

$$Z = c\sqrt{2}\pi R^2 w \quad (3)$$

For the case where $d = R$, this becomes

$$Z = \alpha\sqrt{2}\pi\epsilon^{1/3}cR^{7/3} \quad (4a)$$

whereas for the case suggested by Sundby, $d = c^{-1/3}$, this becomes

$$Z = \alpha\sqrt{2}\pi\epsilon^{1/3}c^{8/9}R^2 \quad (4b)$$

The difference in estimating encounter rates by these 2 methods is proportional to $c^{1/9}R^{1/3}$ and can be moderately large (2- to 3-fold; Kiørboe & MacKenzie 1995, see also Dower et al. 1997). While this difference in estimates may appear appreciable, the uncertainty in parameters, including the choice of α , means that, in practice, it is quite difficult to develop a set of experiments (yet alone field observations) to determine which of these functions is more correct. In essence, the experiment would have to distinguish between a slope of 8/9 and 1 on a $\log(Z)$ versus $\log(c)$ plot. Put otherwise, a 2-fold difference in encounter rate would only appear after a 512-fold change in concentration, all other factors remaining the same.

However, we can disprove the inter-particle separation scale argument by showing that a non-linear de-

pendence of the encounter rate Z on the prey concentration c leads to unacceptable conclusions. Let us consider a simple example. Eq. (4b) indicates that if $d = c^{-1/3}$, for a particular prey concentration c , then $Z_{\text{total}} = c^{8/9}P$, where, for convenience, we use $P = \alpha\sqrt{2}\pi\epsilon^{1/3}R^2$. Now let us consider exactly the same situation, except that now we can distinguish between particles using some biologically and physically non-significant parameter, e.g. half the particles are coloured blue and the other half coloured red. The total concentration remains the same. The concentration of red particles is $c_r = c/2$, which implies, from Eq. (4b), that the predator's encounter rate with red prey items is $Z_r = (c/2)^{8/9}P = 0.54c^{8/9}P$. Likewise, the predator's encounter rate with blue prey items is $Z_b = 0.54c^{8/9}P$. The total encounter rate of the predator with particles of *unspecified* colour is $Z_r + Z_b = 1.08c^{8/9}P$, which is 8% higher than Z_{total} , the encounter rate with particles of *indeterminate* colour. Similarly, 5 different prey items present in equal concentrations would result in an encounter rate 20% higher than if there were only 1 prey item. In other words, the predator's encounter rate depends on the *experimenter's* ability to distinguish between prey items. Clearly, this is an untenable hypothesis.

Our interpretation of spatial scale for turbulent velocity calculations is consistent with other treatments of the turbulent encounter problem (e.g. classical coagulation theory; Kiørboe 1997); the appropriate length scale is determined by the size of the particles involved in the collision. In addition, the author of another study examining the influence of turbulence on planktonic predators arrived at the same conclusion as we have. Osborn (1996) modelled the effect of turbulent diffusion in filter-feeding copepods and showed that the flux of food particles towards the predator was proportional to the extension of the predator's feeding current to the power of 7/3. Indeed, Eq. (14) of Osborn (1996) is identical to our Eq. (4a), with the exception of constants. According to Osborn (1996), 'this same model applies to small fish larvae (Sundby & Fossum 1990), where visual perception replaces the feeding current'.

The correct choice of spatial scale for modelling encounter rates appears therefore to be related to a measure of the predator's ability to detect or perceive prey. This is borne out in the idea of an encounter kernel or clearance rate. Eq. (1) can be recast in the form

$$Z = c\beta$$

where β , the encounter kernel, is a measure of the rate at which the predator perceives a 'new' volume of water. That this rate can be affected by swimming speed and turbulent motion is reasonable. However, using the inter-particle separation distance to define

turbulent velocity scales has 2 important implications. Firstly, this scaling implies that the encounter kernel also depends on the concentration of prey items. That the volume flux of water into the predator's perception volume depends on the number prey items embedded in it is simply insupportable. A second implication is that prey sampling methods will influence the predicted relative effect of turbulence on encounter rates. Plankton distributions are patchy (Owen 1989), and sampling methods are generally scale-specific (Rose & Leggett 1990, Taggart & Frank 1992). Hence, over which spatial scale should prey concentrations be measured to derive a prey separation distance? The choice of sampling methodology for determining the prey concentration will artificially affect predicted encounter rates in turbulent waters via Eq. (4b). A spatial scale for velocity calculations that is based on the larval reactive distance is insensitive to these prey sampling artefacts.

Lastly, while the focus of this note has been on the turbulent velocity at a critical spatial scale (i.e. the larval reactive distance), we stress that all scales within the turbulence spectrum are important contributors to encounter processes. The turbulence contribution at all these scales is expressed in Eq. (2) by the turbulent dissipation rate. Namely, larger and more energetic turbulent eddies mean higher dissipation rates, greater turbulent velocities at all scales, and so higher encounter rates. Small-scale eddies are intimately connected to eddies at larger scales (e.g. Tennekes & Lumley 1972, Denman & Gargett 1995). Secondly, contrary to the assumption inherent in Eq. (1), prey concentrations are generally not uniform (Owen 1989). With respect to this, a question less easily addressed is how larger scale turbulence promotes predator interaction with prey patches, as well as enhancing prey patch dispersion. It is likely that a whole spectrum of interacting turbulence and patch length scales are relevant in these processes (Davis et al. 1991).

Despite our disagreement with Sundby on the choice of spatial scale used in turbulent encounter rate calculations, we share his view that turbulence is an important variable in larval fish and plankton ecology. Nevertheless, turbulent velocity estimates for encounter rate calculations should be derived using larval reactive distance as the relevant spatial scale because this scale has clear theoretical support, is consistent with other mathematical treatments and is more appropriate than any other scaling possibility yet proposed.

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