

in other aspects of zooplankton ecology. The encounter rate calculation is based on the uncorrelated component of the turbulent velocity field. A large fraction of the turbulent velocity field is correlated, particularly when the distance, d , approaches the Kolmogorov scale. We have not paid much attention to how the correlated component of the flow field may affect plankton ecology (Yamazaki 1993).

Despite the fact that we do not know much about the nature of coherent structures, some progress has been made through direct numerical simulation (DNS) of Navier-Stokes equations (Hussain 1986). Squires & Yamazaki (1995) used DNS to follow marine particles in an isotropic turbulent flow. A total of 165 888 particles were placed uniformly at their initial locations. Due to the excess density of the marine particle relative to the ambient fluid, i.e. a particle:ambient fluid density ratio of 1.06, the particles become preferentially concentrated in regions of low vorticity or high strain rate. The peak number density is 40 times larger than the global mean value. If the flow is completely random, this kind of local aggregation cannot take place.

DNS of zooplankton in isotropic turbulence shows that a swimming behavior model based on the local flow strain rate can take advantage of flow structures to sustain the mean vertical position of a negatively buoyant particle (K. D. Squires pers. comm.). The model swimming pattern is controlled by the local rate of velocity strains, and is aligned with the intermediate eigenvector by taking the direction of gravity into account. Since mechanical receptors can detect velocity strain much easier than absolute velocity, the swimming behavior model is a realistic mechanism which conserves biological energy to sustain a negatively buoyant body in a water column.

Since zooplankton have evolved behavioral adaptations to flow patterns, the issue of coherent structures is important. We must realize that the encounter rates problem is not the only effect of turbulence on zooplankton ecology of which we need to be aware.

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Turbulence-induced contact rates in plankton: the issue of scales

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A rapidly increasing quantity of literature has evolved in the wake of the theory developed by Rothschild & Osborn (1988) on the effects of turbulence on plankton contact rates. Although their theory focused on small scales of isotropic turbulence, the general concepts that they proposed are not limited to those scales.

The choice of scale is essential to assessing the effects of turbulence on the interactions between particles in the plankton. Choosing the appropriate scale is dependent upon the relative motion of predator and prey and on the distance between them. However, the fact that turbulence in a natural system occurs simultaneously at all length scales means there is no trivial answer to the question of which of these scales contributes to enhancement of the contact rate between particles. A complete mathematical formulation for this part of the theory on turbulence-induced contact rate is still lacking. However, it follows from physical reasoning that the relevant turbulent length scales are linked to the separation distance, r , between interacting particles.

Turbulent diffusion (or spreading) of particles is the result of the same physical process that causes contact between them, and it is a basic property of turbulent diffusion that the turbulent diffusivity coefficient increases as the size of the diffusing cloud of particles increases (e.g. Okubo 1978). This is so because larger and larger turbulent eddies will take part in the turbulent mixing as the size of the cloud increases. Rothschild & Osborn (1988) developed an expression for the root-mean-square turbulent velocity: $w = 1.9(\varepsilon \cdot d)^{1/3}$ (where ε is turbulent kinetic energy dissipation rate and d is the length scale of the uncorrelated velocity fluctuation). This expression was used to calculate the velocity component of the turbulence-induced contact rate. Since the turbulent eddy diffusivity coefficient is linked to the size of the particle cloud, then, by analogy, the turbulence-induced contact rate between particles is linked to the separation distance between them. Hence, the length scale, d , is proportional to the separation distance r , $d \sim r$, where $r = c^{-1/2}$ is the mean deterministic separation distance between particles at concentration c .

As an approximation for the relevant turbulent scale, d , in the equation above, Sundby & Fossum (1990), Sundby et al. (1994) and Sundby (1995) used $d = r$ in their calculations. More correctly, however, it is really

the sum of all turbulent length scales, d , less than r which contribute to enhancement of the contact rate, because all turbulent scales less than that of the separation distance will change the relative position between the particles and hence contribute to contact. But, since turbulent velocities are larger at the larger length scales, those turbulent velocities generated on the larger length scales contribute more toward increasing the contact rate than do the velocities of the smaller turbulent length scales. Therefore, the error introduced by using $d = r$ is arguably moderate compared to the fact that the contact rate was evaluated over a relatively large range of particle concentrations, from 1 to 50 nauplii l^{-1} , with corresponding separation distances from 10 to 3 cm.

Turbulence at scales considerably larger than the particle separation distance will not, however, contribute to enhancement of the contact rate, since the turbulent 'cells' on these larger length scales will only contribute to the moving around of smaller parcels of fluid without rearranging the positions of the particles within these smaller fluid parcels. The process of turbulence-enhanced contact rate, or the rate of collision between particles, is a physical process which will influence particles in the same way whether they happen to be large or small, biotic or abiotic, dead or alive. For a predator to successfully ingest a prey, however, there are a set of additional biotic processes which must be considered after the prey is located. Here, the reactive distance, R , the maximum distance at which a given prey can be perceived, becomes relevant with respect to the turbulent length scale d . However, R is independent of the preceding physical encounter process, although it enters the calculation of the volume searched by a fish larva as a constant.

Kjørboe & MacKenzie (1995), Kjørboe & Saiz (1995) and MacKenzie & Kjørboe (1995) propose that the predator's reactive distance, R , and not the particle separation distance, r , is the relevant scale over which to evaluate the effects of turbulence on encounter and ingestion. Following the above reasoning, this proposal appears to be based upon the assumption that turbulence only affects the components of the predation cycle that follow prey location. Successful ingestion of prey, however, consists of at least 4 consecutive processes:

(1) *The time required to search for prey prior to encounter or contact.* The search process is the most time consuming part of the predation cycle for many predators, particularly carnivorous plankton (O'Brien et al. 1990). For any kind of interacting vehicles, such as navy vessels (Koopman 1956) or combat airplanes (Kohlas 1967), it is the relative velocity between the vehicles which determines the change in position between them and, hence, the probability of en-

counter. The direct analogy in the animal world is the relative movement between a predator and its prey. For plankton, turbulence adds to the change of relative position between them; and, here, the mean separation distance between the predator and prey is the key parameter determining the scale of relative motion. Hence, and as argued above, during this part of the predation cycle, $d \sim r$

(2) *Prey location time.* This is usually a relatively short interval of time, compared to the search period, during which the predator scans its visual perceptual field for prey and makes the decision to attack or ignore it. Once a prey item has been located, the distance between the predator and prey can be no greater than the reactive distance, R , of the predator. Now, the situation is linked to the one specific prey which has been located, whereas in the search process above the situation was linked to all the surrounding potential prey. The turbulent length scales which in this situation contribute to changes in the relative distance between predator and prey are now all length scales equal to and smaller than R . Hence, $d \sim R$.

(3) *The time of pursuit and attack by the predator and/or escape by the prey.* This time interval, during which the attack occurs, is also quite short. The prey is still no farther from the predator than the reaction distance, R , and therefore the turbulent 'cells' which contribute to changes in the relative distance in this situation are still, as in the situation above, those of length scales equal to or smaller than R . Hence, $d \sim R$.

(4) *The time required to ingest prey.* Predator and prey are no longer separated and the turbulence of the ambient water can, of course, no longer contribute to changes in the relative distance between them. I therefore tend to assume that it is unlikely that turbulence has much effect on this last component of the predation cycle. It could be speculated that very strong accelerations induced by turbulence might cause regurgitation of the prey, but what turbulent scale this might involve is unclear.

When Kjørboe & MacKenzie (1995), Kjørboe & Saiz (1995) and MacKenzie & Kjørboe (1995) only consider the time intervals (2) and (3) as relevant for turbulence-induced encounter rate they neglect the most important and longest time interval of the predation cycle: prey search. However, they also contradict the results of MacKenzie et al. (1994), who proposed a dome-shaped relationship between turbulence and larval fish ingestion rates. MacKenzie et al. (1994) found, conversely, that the effect of turbulence on the scale of reaction distance, R , contributed to a decrease in the encounter rate, not to an increase in it.

Kjørboe & MacKenzie (1995) cite Evans (1989) to support their choice of reactive distance as the correct scale to consider. However, Evans (1989) simply states,

without any further argument, that the appropriate length scale for the uncorrelated component of the turbulent velocity is precisely the encounter radius, R . Kjørboe & Saiz (1995) also cite Delichatsios & Probst (1975) and Hill et al. (1992) to justify the idea that only the smallest turbulent scales are relevant in plankton encounters. However, all of the authors cited in support of this assertion considered closely spaced particles at concentrations several orders of magnitude higher than the abundances which would be realistic, and of relevance, for interactions between larval fish and their prey. Delichatsios & Probst (1975) and Hill et al. (1992) considered only the smallest turbulent scales, around the Kolmogorov scale, in their work on coagulation of very small particles and, hence, their conclusions confirm that the turbulence-induced contact rate is linked to the separation distance between the particles and not to the reaction distance.

There are many implications of relative motion with respect to plankton predator-prey interactions, some of which are linked to behavioral and biological responses (e.g. Rosenthal & Hempel 1970, Browman & O'Brien 1992; see Comments by Browman & Skiftesvik and Strickler & Costello), others of which are related to physical processes. The way in which the cascade of turbulent scales interact depends on the specific process of plankton interaction which is considered.

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Calanoid copepod behavior in turbulent flows

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'...in solving ecological problems we are concerned with what animals do in their capacity as whole, living animals, not as dead animals or as a series of parts of animals. We have next to study the circumstances under which they do these things, and, most important of all, the limiting factors which prevent them from doing other things. By solving these questions it is possible to discover the reasons for the distribution and numbers of different animals in nature.' (Elton 1927).

Since the publication of Rothschild & Osborn's (1988) seminal paper, the influence of small scale turbulence on planktonic encounter rates and, therefore, trophic interactions, has been debated in biological oceanography. Whereas the original model assumed that predators and prey were inanimate points in 3-dimensional space, more recently Osborn (1996, p. 194) concluded that 'treating predators and prey as simple points is not adequate for quantitative predictions'. Clearly, the elevated encounter rates between plankters in a turbulent flow will not result in enhanced trophic exchange unless the zooplankters adapt behaviorally to exploit the high encounter rates. The behavioral response of copepods to turbulence has been the central focus of our work.