Combining Analog Turbulence with Digital Turbulence*

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SUMMARY: Extending the results of laboratory experiments on the interactions between turbulence and phyto- and zoo-plankton to in situ situations requires great skills. Large scale numerical simulations coupled with observations from laboratory experiments in grid turbulence are an appropriate approach for increasing our fundamental understanding of plankton - turbulence interactions. This ‘digital’ approach permits a detailed examination of the flow experienced by individual particles in turbulence. Since zooplankters and algae react mainly to flow conditions within their surrounding water volume, the knowledge gained from this combined approach of simulation and experimentation can be extended to in situ situations.

Key words: Direct numerical simulations, grid-generated turbulence, unsteady flow, plankton.

Physical forcing, chemical activities and the differences in buoyancy between distinct parcels keep water in motion whether it is contained in small vessels in the laboratory or in large geological basins. Calm water is either frozen, heavily stratified or part of an adiabatic and abiotic system. As soon as only one zooplankter swims in the water volume and drags the entrained water mass with it, some water will be in motion. To literally see water in motion, one needs special techniques to visualize flow (NCFMF, 1974). Once one can see the flow and, at the same time, the live suspended algae, the zooplankton and the planktivorous fish (Strickler and Hwang, in press), one can start to comprehend life at the lower level of the food web in ponds, lakes and the seas.

One approach employed in our work has been the in situ deployment of the CritterCam®, an underwater camera system which permits observation of water flow at the places and scales of grazing zooplankters and suspension feeding benthic animals. The CritterCam®, uses matched spatial filters to visualize phase objects at long working distances (Strickler and Hwang, in press). The movements of algae 5 µm and larger and animals of a size up to 5 cm have been videotaped, even if they were totally transparent. The long-working distance of the optics and the use of a near-infrared laser as the light source resulted in non-invasive observations of volumes of water from 10 to 120 ml depending on the magnification. Several hundreds of hours of video tape show a continuous motion of the water.

In spite of the usefulness of these videotaped in situ observations, their interpretation remains
challenging. In order to understand the behavior of the observed animals, it is important to test our interpretations in laboratory experiments under controlled conditions. Since motion of water is one variable to be tested, one has to adhere to the principle of similitude when setting up the experiments (Streeter, 1971). In fluid mechanics, quantitative data are obtained from model studies and applied to the real world if dynamic similitude is given (e.g., same Reynolds number, same Froude number). Recently, Osborn (1996) and Osborn and Scotti (1996) have pointed out that one may have insurmountable difficulties setting up meaningful laboratory experiments on the interactions between turbulence and zooplankton. The question then arises whether there is a way to perform laboratory experiments on these interactions the results of which can be extended to the real world.

In answering this question, we will start with the definition of turbulence and describe earlier thoughts on the interaction between turbulence and plankton. We will then crystallize out a way which we consider safe enough to find solutions in ecological and behavioral investigations on the interactions of turbulence with phyto- and zooplankton.

**TURBULENCE**

Turbulence is an ubiquitous phenomenon occurring in oceans and lakes. Animals and algae living in these environments are more or less affected by the presence of turbulence (Sundby and Fossum, 1990; Granata and Dickey, 1991; Mackenzie and Leggett, 1991). For planktonic calanoids, being small sized, the presence or absence of turbulence may be a deciding factor determining whether their populations will wax or wane (Strickler, 1985). Recent research by Thomas and Gibson (1990) has shown that the growth of a red tide dinoflagellate is negatively affected by turbulence above a dissipation rate of $1.8 \times 10^{-5}$ W/kg. Berdalet (1992) working with different species of dinoflagellates found similar results. Most plankton species experience various intensities of turbulence, e.g., breaking waves induce vigorous stirring near the sea surface. Although the intensity of turbulence is much weaker in the thermocline, a persistent turbulent layer can be found at the interface of two current systems (Yamazaki and Lueck, 1987).

**TURBULENCE** is the most common, the most important and the most complicated kind of fluid motion. It is peculiarly resistant to mathematical treatment: indeed, turbulence studies may be defined as the art of understanding the Navier - Stokes equations without actually solving them.

(Bradshaw, 1971, p. xi)

Despite the fact that the laws governing turbulence -the Navier-Stokes equations- are well known, the non-linearity inherent in these equations renders the details of turbulence dynamics difficult to comprehend. The nonlinear terms in the Navier-Stokes equations are responsible for energy transfer from large to small scales in turbulent flows. This nonlinear transfer proceeds downscale until it is dissipated by viscous effects at the smallest scales of motion. A reference length for small-scale motions can be derived from the intensity of turbulence, which is proportional to the rate of the kinetic energy dissipation, and the fluid viscosity, i.e., the Kolmogorov scale. An observed dissipation rate near the sea surface (Osborn et al., 1992) is $10^{-3}$ W/kg, which corresponds to 0.02 cm for the Kolmogorov scale. In the seasonal thermocline, turbulent layers are patchy and intermittent (Gregg, 1987; Yamazaki and Osborn, 1988; Gargett, 1989). An average rate of the kinetic energy dissipation is roughly $10^{-6}$ W/kg, which corresponds to 0.6 cm for the Kolmogorov scale. A typical length scale of a calanoid is about 0.1 cm, which lies between these two scales. Considering the fact that the laws of physics are universal, one has to wonder how, or by how much, turbulence has influenced and still is influencing the outcome of the Ecological Theater and the Evolutionary Play (Hutchinson, 1965) within the open-water column.

**DEFINITION OF TURBULENCE**

We have so far used the word “turbulence” without attempting its definition. We will follow the suggestion of R.W. Steward, who, in his introductory film on the subject, refers to turbulence in terms of three basic characteristics: disorder (randomness); enhanced mixing; and three-dimensional motions involving angular momentum. We might also add that turbulence occurs at high Reynolds numbers and is generated in the presence of mean velocity gradients.

(Potter and Foss, 1975, p. 307)
Turbulence is a three-dimensional time-dependent motion in which vortex stretching causes velocity fluctuations to spread to all wavelengths between a minimum determined by viscous forces and a maximum determined by boundary conditions of the flow. It is the usual state of fluid motion except at low Reynolds numbers.

(Bradshaw, 1971, p. 17)

MEASUREMENTS AND UNITS

As described above by Bradshaw, turbulence is comprised of a range of length scales; the ratio of the largest scale, $L$, to smallest scale, $\eta$ (the Kolmogorov scale), can be expressed in terms of the Reynolds number (see Tennekes and Lumley, 1972)

$$\frac{L}{\eta} = Re^{3/4}$$

where $Re$ characterizes the ratio of inertial to viscous forces. The above relation clearly shows that, for increasing $Re$ (higher turbulence levels), the separation in the range of length scales rapidly increases. An important statistical measure of turbulence that can be related to both $L$ and $\eta$ is the turbulence dissipation rate, $\varepsilon$. For oceanographic applications, $\varepsilon$ is typically measured in units of W/kg ($1 \text{ W/kg} = 10^4 \text{ cm}^2 / \text{s}^3$). For the large scales, $\varepsilon$ characterizes the rate at which energy is transferred to smaller and smaller scales, while at the smallest scales of motion $\varepsilon$ provides a measure of the energy lost due to viscous effects. Thus, $\varepsilon$ is a statistical measure central to characterizing turbulence and explains, for example, why physical oceanographers use it as the primary measure to define the level of turbulence in the upper ocean. The importance of the dissipation rate for examining small-scale interactions is that, together with the fluid viscosity ($\nu$), it can be used to estimate the size of the smallest turbulence length scale - the Kolmogorov scale, $\eta$:

$$\eta = (\nu^3 / \varepsilon)^{1/4}$$

In order to estimate $\eta$, one must be able to infer the dissipation rate of the flow. This is straightforward in Direct Numerical Simulations; in experiments there are other reliable means which may be used to measure $\varepsilon$ (e.g., Marrasé et al., 1990; Hill et al., 1992).

PARADIGM SHIFT IN THE PERCEPTION OF TURBULENCE

Traditionally, turbulence has been thought of as a nearly random process which causes much higher diffusion than that achieved solely by molecular effects (see definitions above). However, it is now known that there are local regions in a turbulent flow which are not completely random. Both experimental measurements and numerical simulations of turbulent flows clearly show evidence of “organized”, or “coherent” structures. These “organized” structures play a major role in the dynamics of turbulence (Hussain, 1986). Vortex tube formations provide an example of such “organized” structures (Vincent and Meneguzzi, 1991).

Various algorithms have been developed for characterizing the different regions of a turbulent flow, e.g., Hunt, Wray and Moin’s (1988) classification of ‘eddies’, ‘streams’, ‘rotational zones’, and ‘convergence zones’. Using the database generated from Direct Numerical Simulations (DNS) of homogeneous turbulence and fully-developed turbulent channel flow, Hunt et al. (1988) demonstrated that these identifiable, coherent structures are responsible for a large fraction of momentum transport and turbulence dissipation (see also the later work of Wray and Hunt, 1989). The facility of DNS makes the above remark (see Bradshaw, 1971) about the Navier-Stokes equations mute. However, despite the increasing availability of DNS techniques which may be run on personal workstation (e.g., see Squires and Yamazaki, 1993), it remains a challenge to understand and interpret solutions of the Navier-Stokes equations.

UNSTEADY FLOW VERSUS TURBULENCE

The term turbulence has its definition in fluid mechanics (see above). N. Oakey (pers. comm.) suggested that biologists should refer to “turbulence” only when these conditions are met. In addition, Osborn (1996) remarked that to observe in the laboratory animals reacting to “turbulence” is almost meaningless because no laboratory setup allows the inclusion of all spatial and temporal scales necessary to investigate the effects of true-blue turbulence on planktonic life, $L$ is too small and, hence, the range of Reynolds numbers attainable in the laboratory are smaller than in the field.
Here, we suggest that future biologists should carefully consider the distinctions between unsteady flow and turbulence, especially when the water flow in question may not meet the above conditions and, therefore, the definition of turbulence. However, when referring to older literature we will still use the term “turbulence” but in quotation marks.

UNSTEADY FLOW AND THE SHAPES OF PLANKTONIC ORGANISMS

Turbulence, or unsteady flow, has been the topic of thought experiments on the interactions between plankton and the surrounding water for many years. For example, Einsele and Grim (1938) argued that turbulence may sort algal populations in the water column according to the specific gravity of the different algal species. Strong turbulence may keep “heavy” algae suspended whereas in zones of weak to no turbulence they would sink faster than “lighter” algae. In this way, the authors explain the presence of “heavy” diatoms in the upper, turbulent layers of the water column and the dominance of smaller algae in the lower part of the column.

Margalef (1978) constructed a different train of thought. Not only are algae suspended in the water column but also their nutrients. Both are sinking to the lower layers due to gravity. However, for growth, algae need to be in the upper layers where sufficient light is available. The addition of physical forcing which introduces water motion, and in turn turbulence, to the water column will counter this sinking trend away from the light. The different “life-forms” contained in the phytoplankton may represent the results of evolutionary and ecological responses to the accessibility of nutrients, light, and sinking rates based on the shapes and mobility of the algae (see Fig. 2 in Margalef, 1978).

Experimenting with Daphnia, Brooks (1947) observed that the animals will grow larger helmets when reared under conditions with “turbulence” than in vessels without stirring. However, animals which grew up in nature showed even larger helmets. This cyclomorphosis, seasonal changes in allometric growth, has been a topic for debate for many years (Wesenberg-Lund, 1900; Woltereck, 1913). Brooks’ results were confirmed by Hrbacek (1959) and Jacobs (1961). With the discovery that chemicals emitted by the predators of the cladocerans induce cyclomorphosis (e.g., Grant and Bayly, 1981; Krueger and Dodson, 1981), Jacobs (1987) concluded that further work on environmentally stimulated induction might seem redundant. Turbulence may, however, still be an agent: it could transport the chemicals from the predators to the cladocerans faster than molecular diffusion would do. In addition, cladocerans may not find as fast a refuge from their predators and may have to counteract the increase in encounter rate between them and their predators by the additions of anti-predatory devices.

TURBULENCE AS ENHANCER OF ENCOUNTER RATES

Turbulence increases the encounter rates between predators and their prey as shown theoretically by Rothschild and Osborn (1988). Their contribution stimulated a plethora of research giving rise to many answers and even more questions. Recently, a whole discussion section in the Marine Ecology Progress Series has been dedicated to the topic (Browman, 1996; Browman and Shiftesvik, 1996; Osborn and Scotti, 1996; Strickler and Costello, 1996; Sundby, 1996; Yamazaki, 1996). Earlier, Osborn (1996) modified the encounter model to include feeding currents of grazing calanoid copepods. This was necessary because so many zooplankters and most phytoplankters are small enough to “hide” in the Kolmogorov scale (e.g., Granata and Dickey, 1991; Haury and Yamazaki, 1995; Yamazaki, 1996) and are, therefore, not fully exposed to the turbulent motion. However, when feeding currents are included, turbulence will increase the supply of food to calanoid zooplankters.

The notion that turbulence increases the encounter rate between algae and calanoid copepods was the basis for the research of Costello et al. (1990) and Marrasé et al. (1990). In their experiments, the animals were tethered and exposed to unsteady flow. The observations included the paths of the algae, as well as, the behaviors of the animals over a period of two hours. Besides counting the number of algae entering the capture area per unit time (encounter rate; see Costello et al., 1990), it was also possible to analyze the encounter rates of virtual animals by counting the number of algae entering a space of equal size to the capture area somewhere distant from the real animal. The ratio between the virtual and the real encounter rates then gives a measure of the efficacy of the feeding current (Marrasé et al., 1990).
Tethered animals experience unsteady water flow and turbulence differently than free-swimming animals. They cannot float with the larger motion of the water and are exposed to much more severe changes of flow conditions surrounding their bodies (Osborn, 1996). The starting point for Costello et al. (1990) and Marrasé et al. (1990), who used tethered copepods, was to set up the most extreme conditions in order to find out whether the animals behave in an “orderly” fashion when exposed to unsteady flow. All they knew at that time was that zooplankters react with escape reactions when exposed to strain and vorticity (e.g., Strickler and Bal, 1973; Strickler, 1975; Wong, 1980; Zaret, 1980; Haury et al., 1980). To the surprise of the researchers, the animals, after an initial period of escape reactions, increased and maintained their feeding activities even when the unsteady flow subsided. Later, several laboratory experiments were carried out with free-swimming animals. Saiz and Alcaraz (1992), working with untethered individuals of *Acartia clausi*, found significant behavioral differences when comparing calm and turbulent conditions. Other experiments have been performed with different species of *Acartia* to study the effect of turbulence in terms of feeding and gross-growth efficiency. These experiments showed that the responses to turbulence depended on the particular species (Saiz et al., 1992), and the differential response seemed to be related to the physical characteristics of natural environment from which the species came. In addition, several studies have shown that the relative importance of turbulence correlates with the feeding modes of planktonic organisms (Saiz and Kiørboe, 1995, Kiørboe and Saiz, 1995). Therefore, one could conclude that at least some zooplankton species are adapted to turbulence in their natural environment and do take advantage of the increased encounter rates.

In future research, the arguments of Osborn (1996) have to be taken into account. The question then is how would one conduct experiments on the topic of turbulence and feeding performance? These experiments should parallel the ones conducted in calm water by Paffenhöfer et al. (1995). These authors observed not only the encounter rates of free-swimming calanoids but also precise time series of algae eaten or rejected and the production of fecal pellets. As mentioned above, to observe similar time series in situ may be a very challenging proposition but should be attempted. However, such in situ observations still do not give the researchers the tools to control the parameters of the experiments. How would one then approach this topic in the laboratory taking similitude into account?

One feasible approach can be to tie studies (see Cipra, 1995) using grid-generated turbulence in a vessel (zero-mean-flow turbulence, e.g., Dickey and Mellor, 1980; De Silva and Fernando, 1992; Hill et al., 1992) with DNS (digital turbulence; e.g., Squires and Eaton, 1991; Karwadiakis and Orszag, 1993). We consider this approach, combining analog with digital turbulence, feasible because suspended particles such as algae and zooplankters do not perceive with their sensory systems the full spatial and temporal scales of turbulence. This approach is limited to the observations of small volumes of water (e.g., 80 l) and would not render direct observations of large ecological systems like swarms of copepods or juvenile fish. However, it can help us to fathom the behavior of individual animals and algae when suspended in a turbulent flow.

**DIGITAL AND ANALOG TURBULENCE**

Direct Numerical Simulation of the incompressible Navier-Stokes equations can be used for generating digital turbulence. In DNS the time-dependent, incompressible, Navier-Stokes equations are solved for canonical flows, e.g., homogeneous turbulence. Since homogeneous turbulence is in principle unbounded, periodic conditions are used in the calculations. The spatial domain must then be large enough to contain an adequate sample of large eddies whose spatial correlation decays to zero in a length small compared to the size of the domain. A large fraction of turbulence simulations are based on the elegant pseudo-spectral method developed by Rogallo (1981), in which spatial differentiation is performed using Fourier series and de-aliasing is accomplished using a novel combination of coordinate shifting and truncation.

Flow fields computed in DNS and relevant to laboratory experiments are of “grid turbulence”, i.e., the analogous flow measured in the laboratory is turbulence generated behind an oscillating grid. In the majority of grid-turbulence experiments and computations Reynolds numbers, based on the Taylor microscale, vary between about 30 and 80 (e.g., Comte-Bellot and Corrsin, 1971; Warhaft and Lumley, 1978; Veeravalli, 1991), with the lower end of this range corresponding to those flows which can be economically simulated using DNS (DNS calcu-
lutions of isotropic turbulence have been performed up to Reynolds numbers of 170 using high performance parallel computers, e.g., see Jimenez et al., 1993). The lower end of the Reynolds number range corresponds to those that are most easily and practically obtained in turbulence experiments performed using water vessels with oscillating grids (e.g., Dickey et al., 1984). Aside from ensuring an adequate sample of large-scale motions, it is also required in DNS that grid spacings be fine enough to accurately resolve small-scale motions. Previous work has shown that quantities such as $k_{\text{max}} \eta$ ($k_{\text{max}}$ is the maximum wave number of the computation and $\eta$ is the Kolmogorov length scale) need to be at least greater than 1 for accurate small-scale resolution.

From an initial spectrum, in DNS the flow evolves as dictated by the Navier-Stokes equations. Interfacing DNS with experimental measurements on grid turbulence requires matching the dissipation rate and Reynolds number. Because of the limited range of scales in DNS, as well as in the majority of oscillating grid experiments, dissipation rates in the range $10^8$ to $10^5$ are attainable in DNS using moderate grid resolutions. While calculations for the same range of Reynolds numbers and dissipation rates is feasible in DNS compared to experiments, in oscillating grid experiments the flow is non-homogeneous between planes parallel to the grid. In DNS the entire three-dimensional volume is statistically homogeneous and, therefore, it is important to obtain measurements in several planes of the vessel in order to determine any effects of the spatially non-homogeneous direction on measurements.

A key feature of DNS calculations is the ability to obtain Lagrangian information, i.e., following individual particles in the flow. For particles with finite inertia, motion is described through solution of the equation of motion as derived by Maxey and Riley (1983). For particles with very small inertia their motion is essentially the same as that of a fluid point at the instantaneous particle position. In either case accurate and efficient interpolation schemes can be used to obtain the fluid velocity at the particle position, which is necessary for advancing the position of the particle. Acquiring information following copepods and algae in a laboratory vessel is more difficult than in DNS, but modern optical techniques now permit accurate measurements of particle trajectories and velocities (e.g., Marrasé et al., 1990). DNS calculations can in turn provide information and insight as to the nature of the flow experienced by the particle, e.g., strain rate following the particle.

It is important to stress that the most important aspect of interfacing DNS with laboratory experiments is verifying simulation results through comparison to experiments. Time histories of particle velocities, dissipation rate, and the Reynolds number are important descriptors necessary for assessing the compatibility between DNS and experiments. Correlation measurements following particles can then be extracted from the DNS to more clearly understand the flow experienced by particles in the laboratory vessel. Experimental measurements can then be used to formulate, for example, simple swimming models based on animal’s responses to the local flow (e.g., Keiyu et al., 1994). Such models will be valuable for increasing our understanding of copepod interactions with turbulence as well as providing a database for improving lower-level models.

Finally, let us consider briefly our original question whether results from laboratory experiments on the interactions between turbulence and algae and their grazers can be extended to the real world. First, while ‘fine-tuning’ the digital turbulence to represent our analog turbulence, we learned where our analog turbulence deviates from theory. Second, when, for example, an animal regularly switches its behavior under particular conditions in the laboratory, we can examine and describe the local flow conditions of this behavioral switch. Third, given a large catalogue of such descriptions, we can then interpret in situ observations and design field experiments for verification. Similitude is given because the combination of analog with digital turbulence permits description of a whole set of parameters governing the swimming behaviors at the temporal and spatial scales of the animals in question.

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