SMALL-SCALE PHYSICAL PROCESSES AND PLANKTON BIOLOGY

J. F. Dower, University of British Columbia,
Vancouver, BC, Canada
K. L. Denman, University of Victoria,
Victoria BC, Canada

doi:10.1006/rwos.2001.0209

Introduction

By definition, plankton are aquatic organisms (including plants, animals, and microbes) that drift in the water and which cannot swim against any appreciable current. Most plankton are also very small, usually much less than 1 cm in size. Thus, it should come as no surprise that the behavior of, and the interactions between, individual plankton are strongly influenced by small-scale physical processes. Although this may seem intuitive, the fact is that oceanographers have only been aware of the importance of small-scale physical processes to plankton ecology for about the past 20 years, and have only been able to directly study plankton biology at these scales for the past 10 years or so. The primary reason for this is that the space and time-scales relevant to individual plankton (millimeters → meters, and seconds → hours) are quite small, making it extremely difficult to sample properly in the oceans. Thus, much of what we know about the effect of small-scale physical processes on plankton biology is necessarily based on empirical and theoretical studies.

One might well ask why we need to understand the behavior of individual plankton at all, especially given that traditional plankton ecology (at least as conducted in field studies) generally involves comparisons between averages. For instance, we usually compare differences in the average zooplankton density or the average rate of primary productivity at several sites. However, in comparing averages, researchers make many implicit (though often unstated) assumptions about the behavior of the individual plankton that comprise these populations. Specifically, researchers assume that differences in average population-level responses are merely the sum of many individual responses. But is this a realistic assumption? To explore this idea, let us consider what individual planktonic organisms actually ‘do’ and examine how they are affected by small-scale physical processes.

Life in the Plankton

First, let us consider a typical phytoplankton cell. We will assume it is a large (e.g., 100 μm) diatom. In the simplest sense, the biological processes of prime importance to this organism are that of finding sufficient light and nutrients to photosynthesize, grow, and reproduce, while at the same time trying to avoid sinking and predation. Next, let us consider a typical zooplanktonic organism. We will assume it is a copepod. What does it actually ‘do’? On a daily basis it spends much of its time searching for food. Once food is encountered it must then be captured and ingested. In the meantime, this copepod must also try to avoid its own predators. Toward these goals of predator avoidance and feeding, certain zooplankton (including many copepods) also undertake diel vertical migrations of hundreds of meters (for more details on diel vertical migrations). Assuming our copepod reaches maturity (having successfully avoided being eaten) it must then find a mate in order to reproduce. Finally, like the diatom cell, our copepod must also try to avoid sinking. How might these various biological processes be affected by small-scale physics? There are two main factors that must be considered: viscosity and turbulence. Interestingly, both are related to the interaction between the very small size of most plankton, and the nature of the fluid environment that they inhabit.

Effects of Viscosity

The first thing to consider is that, although they live in open water and are transported by the background flow, the world probably feels quite ‘sticky’ to most plankton. This is due to the fact that at very small spatial scales and at the relatively slow swimming speeds or sinking rates of most plankton (i.e., of order mm s^{-1}), viscous forces dominate over inertial forces. The relative importance of viscous to inertial forces can be determined by calculating a dimensionless quantity known as the Reynolds number:

$$Re = \ell U/v \qquad [1]$$

where ℓ is the characteristic length (m) of the object in question, U is the speed (m s^{-1}) at which the object is moving, and v is the kinematic viscosity (m^2 s^{-1}) of the medium in which the object is

Table 1 Approximate value of Reynolds numbers for the swimming speeds of various animals. Note that the kinematic viscosity was taken as $1.05 \times 10^{-6}\,m^2\,s^{-1}$, which approximates that of sea water at 20°C

Animal	*Length (m)*	*Speed ($m\,s^{-1}$)*	*Re*
Whale	20	10	200 000 000
Tuna	2	10	20 000 000
Human	2	2	4 000 000
Small adult fish	0.5	0.5	240 000
Post-metamorphosis fish	0.05	0.05	2400
Larval fish	0.005	0.005	24
Adult copepod	0.002	0.02	4

moving. For our purposes we will take $v = 1.05 \times 10^{-6}$, a value typical of sea water at about 20°C.

When $Re > 2000$, inertial forces dominate and the flow is turbulent. For values of $Re < 2000$ viscous forces become progressively more important. Note that *Re* is not meant to be a precise measure, serving merely as a 'ballpark measure' for comparing the flow regimes that apply to different objects. **Table 1** lists some estimates of *Re* that apply to the swimming motions of various animals. Note that for most plankton, *Re* is generally less than 100, meaning that flow conditions are strongly viscous. Thus, once active swimming ceases, instead of continuing to glide (as does an adult fish once it ceases swimming), the low Reynolds numbers that apply to most plankton ensure that they come to an almost immediate stop.

There is at least one notable exception to this, however; the escape responses initiated by certain copepods. Copepods are equipped with antennae that serve as highly sensitive mechanoreceptors. In addition to detecting food and potential mates, these mechanoreceptors can also warn of approaching predators. Recent work has shown that some copepods can initiate escape responses (a series of rapid hops in a direction away from the perceived threat) in < 10 ms. Moreover, they can achieve burst speeds of several hundred body lengths per second. In some cases, the acceleration achieved is sufficient to enable the copepod to break through the 'viscous barrier' and enter the inertial world, albeit temporarily. Some copepod species have even evolved myelinated axons in their antennae to boost signal conduction along the nerves responsible for initiating the escape response.

Effects of Turbulence

Although occasionally occurring in very dense patches most zooplankton are actually rather dilute. Concentrations of $10\text{–}100\,l^{-1}$ are typical for many neritic copepods, and concentrations of planktonic organisms such as jellyfish and larval fish are usually orders of magnitude lower still (e.g. 1 per $10\text{–}100\,m^3$). Thus, given these low concentrations, it has long been (and continues to be) widely held that food concentrations in the ocean are limiting to growth and biological production. Throughout the 1960s and 1970s this belief was strengthened by the observation that successfully rearing copepods and larval fish in the lab often required food concentrations several times higher than those encountered in the oceans.

The point to consider, however, is that at the sub-meter scales relevant to most plankton, water motions tend to be dominated by random turbulence rather than directional flow. Turbulence is a ubiquitous feature of the ocean, and exists at all scales. In the surface layer of the ocean turbulent energy usually comes from the mixing effects of winds, or from the current shear between layers of water moving in different directions. In shallow coastal waters a second source of turbulence is tidal friction with the seafloor, which stirs the water column from the bottom up. From the perspective of our individual plankton, the key point is that in the surface layer of the ocean these small-scale turbulent velocities tend to be of the same order of magnitude as (or larger than) the typical swimming and/or sinking velocities of most plankton. How will this affect interactions between individual plankton?

Turbulence and Predator–Prey Interactions

Until the late 1980s, the contact rate between planktonic predators and prey was usually expressed as a simple function of (1) the relative swimming velocities of the predator and its prey, and (2) the prey concentration. Put simply, the faster predator and prey swim, and the higher the prey concentration, the more often should the predator and prey randomly encounter each other. Numerically, this can be represented as:

$$Z = D \times A \qquad [2]$$

where Z is the encounter rate, D is the prey density, and A is the relative velocity term. However, in 1988 researchers first theorized that small-scale turbulence might play an important role in predator–prey interactions in the plankton. Specifically, it was hypothesized that small-scale turbulent motions can randomly bring predator and prey together in the water column and, thus, that D and A from eqn. 2 should be rewritten as follows:

$$D = \pi R^2 N \qquad [3]$$

and

$$A = (u^2 + 3v^2 + 4w^4)/\surd 3(v^2 + w^2) \qquad [4]$$

where R is the distance at which the predator can detect the prey (m), N is the prey concentration (m^{-3}), u and v are the prey and predator swimming speeds ($\mathrm{m\,s}^{-1}$), and w is the turbulent velocity ($\mathrm{m\,s}^{-1}$). Eqn. [3] assumes that the predator searches a circular area in front of itself, the result being that as it swims forward its 'search volume' assumes the shape of a cylindrical tube of radius R. In fact, this is only one of many search geometries displayed by visual planktonic predators. For instance, although some larval fish (e.g., herring larvae) are 'cruise predators' and scan a cylinder of water as described above, laboratory experiments have also shown that other species (e.g., cod larvae) are better described as 'pause–travel' predators. In this case, the predator searches for prey only during short pauses. These are followed by short bursts of swimming, during which there is no searching. Furthermore, the geometry of the volume searched also appears to be species specific, although in general it assumes the shape of a 'pie-shaped wedge' centered along the predator's line of vision.

There are also many predatory zooplankton that do not rely on vision at all. These include mechanoreceptor predators (e.g., raptorial copepods, chaetognaths) which detect the vibrations and hydrodynamic disturbances created by approaching prey, and contact predators (e.g., jellyfish, ctenophores) armed with stinging or entangling tentacles and which essentially rely on prey bumping into them. There are also a wide variety of filter-feeding (e.g., copepods, larvaceans) and suspension feeding zooplankton (e.g., heteropods) which generally feed on phytoplankton and protozoans that are either strained out of a feeding current or which are ingested after becoming trapped on mucus coated surfaces.

Regardless of the search geometry and mode of feeding, however, the general hypothesis is that as turbulence increases so, too, should encounter rates between predator and prey. Among the chief reasons plankton ecologists are interested in this idea is the longstanding belief that food availability is an important regulator of the growth and survival of zooplankton and larval fish. Throughout the 1990s, researchers sought empirical evidence of this phenomenon. A number of laboratory studies did show that copepods encounter more prey under increased turbulence. These experiments also showed that many copepods initially respond to increased turbulence by initiating escape responses. The explanation of this result was that, being mechanoreceptor (rather than visual) predators, copepods initially interpret an abrupt increase in turbulence as signaling the approach of a potential predator. Other laboratory studies have since demonstrated that larval fish also initiate more attacks and have higher levels of gut fullness under increased turbulence.

Of course, there are limitations to what can be modeled realistically in any laboratory study, especially those studying small-scale physical processes. For instance, the experiments described above typically involved videotaping the behavior of individual copepods that had been tethered in a flow field in which the turbulence could be varied. It remains to be seen whether the behavior of such tethered animals is the same as that of free-swimming copepods. Likewise, experiments on the effect of turbulence on larval fish feeding ecology usually involve offering only a single type and size of prey at a time, and usually at unrealistically high prey concentrations (e.g. 1000s of prey per liter). In the ocean, of course, larval fish encounter a wide range of prey types and prey sizes, many of which typically occur at relatively low concentrations.

Logistically, the biggest challenge is that of trying to create a realistic turbulent field under laboratory conditions. The small size of most plankton necessitates the use of rather small volume aquaria for experimentation, especially if (as is often the case) the goal is to use videographic techniques to follow individual plankton. Such experiments generally rely on variable speed oscillating grids or paddles to generate different levels of turbulence. Thus, although empirical studies have taught us a lot about the potential importance of turbulence in plankton ecology, the question remains as to whether this process is actually important in the ocean.

Further refinements of the theory have since suggested that the relationship between turbulence and feeding success should be dome-shaped (rather than linear) since, at some point, the predator will be unable to react to prey before they are carried away by high levels of turbulence (**Figure 1**). However,

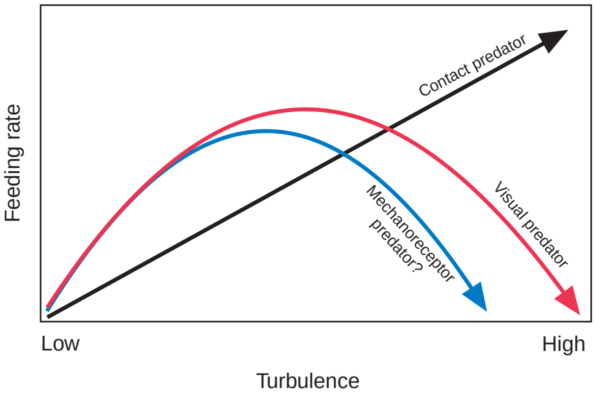

Figure 1 Possible responses of a visual predator, a mechanoreceptor predator, and a contact predator to turbulence. The domed response of visual predators such as larval fish has been supported by laboratory studies. The other two lines are more speculative. The linear increase proposed for contact predators (e.g. jellyfish and ctenophores) is based on the premise that these predators rely on prey bumping into them. However, given that mechanoreceptor predators such as raptorial copepods actually 'hear' the turbulence, it may well be that their ability to separate the signal of an approaching prey item from that of the background turbulent noise declines at higher turbulence levels, leading to a lower optimum level of turbulence than for the other types of predators.

this theory is based largely on the assumption of a visual predator. It remains to be seen how other types of planktonic predators should respond to turbulence. For instance, will the functional response of a mechanoreceptor predator (e.g., a raptorial copepod) be dome-shaped, too? Perhaps such a predator should have a lower 'optimum' level of turbulence than a visual predator since, at high turbulence levels, the background turbulence might make it more difficult to sense prey? Similarly, perhaps a linear response should be expected for 'contact predators' such as jellyfish or ctenophores. Further laboratory work will be needed to clarify this matter.

There have been some attempts to quantify the effect of turbulence on zooplankton and larval fish in the field. To date, although the evidence broadly suggests that turbulence increases encounter rates and even gut fullness (**Figure 2**), its effect on the growth and survival rates of larval fish and zooplankton remains uncertain. What is known is that not all species respond to turbulence in the same way. For instance, although gut fullness in larval Atlantic cod (*Gadus morhua*) and radiated shanny (*Ulvaria subbifurcata*) increases in response to increased turbulence, other species such as herring (*Clupea harengus*) and walleye pollock (*Theragra chalcogramma*) actively move deeper in the water column to avoid turbulence during windy conditions. Similarly, field observations demonstrate that the vertical segregation of at least two congeneric copepod species (*Neocalanus cristatus* and *Neocalanus plumchrus*) is determined by species-specific preferences for different turbulent regimes. Such responses make it extremely difficult to generalize whether turbulence is of net positive benefit to zooplanktonic predators.

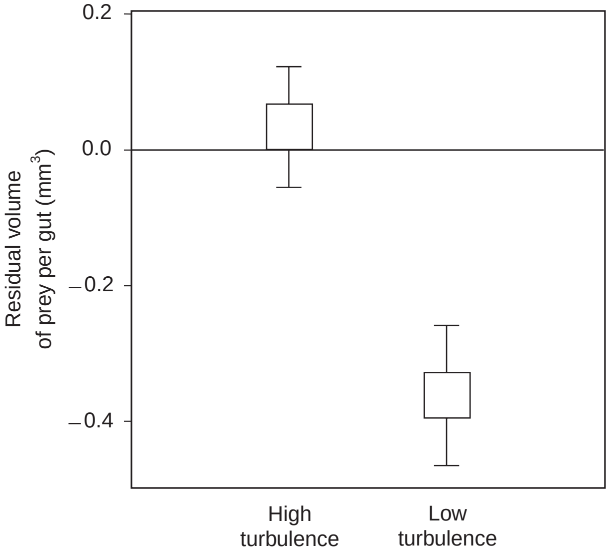

Figure 2 The effect of turbulence on gut fullness in larval radiated shanny *(Ulvaria subbifurcata*) during a 23-day time-series in July/August 1995 in coastal Newfoundland. Despite the fact that prey concentrations remained relatively constant throughout, the figure shows that the average volume of food in the guts of larval fish was significantly higher on high turbulence days than on low turbulence days. Note that the data have been detrended, since larger larvae will generally always have more food in their guts than smaller larvae. The figure thus shows the residual volume of food per gut (i.e., after the size effect has been removed). (Redrawn from Dower *et al.*, 1998.).

Turbulence and Reproductive Ecology

In addition to its effect on feeding ecology, turbulence also appears to play a role in zooplankton reproduction. Recent work has shown that the males of some copepod species find mates by following chemical 'odor trails' left by the females. High-resolution videographic observations show the male swimming back and forth until he crosses the odor trail, at which point he immediately reverses direction to pick up the trail again. Having locked onto the trail the male then follows it back to the female (**Figure 3**). Should the male initially head the wrong way down the trail, he quickly reverses direction and goes the right way until reaching the female.

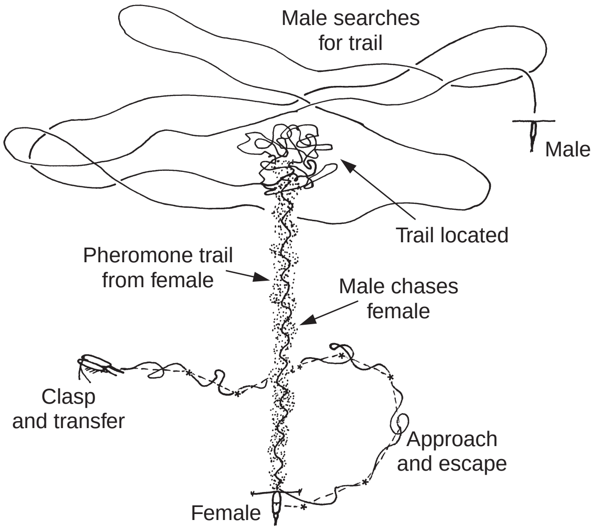

Figure 3 Conceptual interpretation of mate-attraction and mate-searching behavior in the copepod *Calanus marshallae*. The sequence of events first involves the female producing a pheromone trail, which alerts the male that a female is in the area. The male initially swims in smooth horizontal loops until he crosses the trail. At this point the male follows the trail back to the female. (Redrawn from Tsuda and Miller (1998) and used with the kind permission of the authors.).

Turbulence comes into play because the odor trails persist for only a few seconds before being dissipated by small-scale turbulent motions, making it harder for the males to find females. Although it has yet to be confirmed in the lab, this may partly explain why many zooplankton form dense swarms during mating. If the males are to successfully find females via odor trails it might be predicted that mating swarms should be dense enough that the time taken to randomly encounter an odor trail is shorter than the time taken for the trails to dissipate. It is also known that copepod species that usually inhabit the near-surface layers of the ocean often descend to depths of hundreds of meters to reproduce. Is it possible that this behavior is partly a response to the need for relatively quiescent waters in order to allow males to track females before odor trails are dissipated by small-scale turbulent motions?

Turbulence and Phytoplankton Ecology

Recall our typical diatom. Like other phytoplankton, it needs to stay relatively close to the surface in order to capture sufficient light for photosynthesis. Phytoplankton have evolved a variety of adaptations to reduce sinking, including the production of spines and other external ornamentations (to increase drag), the inclusion of oil droplets (to increase buoyancy), and the evolution of hydrodynamic geometries that induce ‘side-slipping’ (as opposed to vertical sinking). Despite all these adaptations, however, many phytoplankton, particularly the larger diatoms with their relatively heavy siliceous frustules, still rely on turbulent mixing to remain suspended in the water column. It has also been shown that turbulence plays an important role in determining the taxonomic composition of phytoplankton communities. For instance, the phytoplankton communities of upwelling zones are usually dominated by large diatoms, whereas less turbulent regions (e.g., open ocean) are more often dominated by much smaller phytoplankton taxa. Similarly, and particularly at temperate latitudes where there is a strong seasonality in wind-mixing, there is often a seasonal succession of phytoplankton species in coastal waters whereby large diatoms dominate during the spring bloom when winds, and thus near-surface turbulent mixing, are strongest. As the summer progresses, and stratification of the upper water column proceeds, large diatoms are often succeeded by more motile forms (e.g., dinoflagellates and coccolithophores) and smaller phytoplankton (e.g., cyanobacteria) that rely less on turbulence to remain near the surface.

A growing body of literature suggests that turbulence can also have novel effects on dinoflagellates. Many dinoflagellate species are bioluminescent, producing a flash of light when disturbed. Recent work has revealed that such bioluminescence may provide an indirect means of reducing predation. Experiments show that some dinoflagellates only bioluminesce in response to strong current shear, such as that induced by breaking surface waves or by predators attempting to capture them. The so-called ‘burglar alarm’ theory suggests that, by flashing in response to strong shear and lighting up the water around themselves, the dinoflagellates make their potential predators more visible, and thereby more prone to predation from *their* predators. This effect has been demonstrated in the lab, where species of squid and fish (feeding on mysids, shrimp, and other fish species) have been observed to increase their rates of attack and capture success when the water in which they are foraging contains bioluminescent dinoflagellates. Apparently, prey movements induce the dinoflagellates to flash, thereby illuminating the prey and making it easier for the predator to capture them.

Turbulence has also been shown to have negative effects on dinoflagellates. It has long been known that dinoflagellate blooms are most common when conditions are calm. However, recent work has shown that even moderate amounts of turbulent mixing can actually inhibit the growth of certain dinoflagellates. The effect seems to be that of preventing cell division, since other cellular processes (e.g., photosynthesis, pigment synthesis, nucleic acid synthesis) appear to continue as usual. If the period of turbulent mixing is short-lived, the cells recover and quickly begin dividing, possibly going on to form a bloom. If, however, the turbulence continues for longer periods, the cells will be prevented from dividing, or they may even die. Of particular interest is that the growth of at least two dinoflagellate species that form harmful algal blooms *(Lingulodinium polyedrum* and *Heterosigma carterae*) seems to be inhibited by turbulence.

Conclusions

Although our basic view of plankton as being organisms that 'go with the flow' still holds true, over the past 20 years we have also learned that interactions between plankton and their physical environment can be quite complex. Perhaps the most important result of this research has been the realization that small-scale physical processes affect so many different aspects of plankton ecology including feeding, predator–prey interactions, swimming and buoyancy, nutrient diffusion, mate selection, and even patterns of community composition. That many of these discoveries are rather new is largely due to the fact that, until relatively recently, oceanographers were simply unable to conduct experiments and observe plankton at appropriately small scales. Now that we have that capability, however, the challenge in the coming years will be to find ways to integrate what has been learned about the behavior of individual plankton to further develop our understanding of population-level processes. Are population-level processes merely the sum of innumerable individual interactions, or are there other physical processes that affect populations at larger space and timescales? Alas, we do not yet know the answer to this question. However, finding new ways to extend what has been learned in the laboratory into more realistic field settings may prove one step in the right direction.

See also

Fish Larvae. Plankton.

Further Reading

Berdalet E (1992) Effects of turbulence on the marine dinoflagellate *Gymnodinium nelsonii*. *Journal of Phycology* 28: 267–272.

Dower JF, Miller TJ and Leggett WC (1997) The role of microscale turbulence in the feeding ecology of larval fish. *Advances in Marine Biology* 31: 170–220.

Dower JF, Pepin P and Leggett WC (1998) Enhanced gut fullness and an apparent shift in size selectivity by radiated shanny (*Ulvaria subbifurcata*) larvae in response to increased turbulence. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 128–142.

Fuiman LA and Batty RS (1997) What a drag it is getting cold: partitioning the physical and physiological effects of temperature on fish swimming. *Journal of Experimental Biology* 200: 1745–1755.

Kiorboe T (1993) Turbulence, phytoplankton cell size, and the structure of pelagic food webs. *Advances in Marine Biology* 29: 1–72.

Mensinger AF and Case JF (1992) Dinoflagellate luminescence increases susceptibility of zooplankton to teleost predation. *Marine Biology* 112: 207–210.

Rothschild BJ and Osborn TR (1988) Small-scale turbulence and plankton contact rates. *Journal of Plankton Research* 10: 465–474.

Tsuda A and Miller CB (1998) Mate-finding behaviour in *Calanus marshallae* Frost. *Philosophical Transactions of the Royal Society of London*, B 353: 713–720.

Vogel S (1989) *Life in Moving Fluids: The Physical Biology of Flow*, 3rd edn. Princeton, NJ: Princeton University Press.

SOMALI CURRENT

M. Fieux, Université-Pierre et Marie Curie,
Paris, France

doi:10.1006/rwos.2001.0364

Introduction

The western Indian Ocean is the only region of the world where a large boundary current, as strong as the Gulf Stream, reverses twice a year in response to the wind reversals during the north-east winter monsoon and the south-west summer monsoon. This region of the Somali current is known to undergo the highest variability of the world ocean circulation.

Along the Somali coast, the reversals of winds and currents, known for many centuries, have been used by the Arabic traders for their navigation along the African coast and towards India. The term