

"Water is life's mater and matrix, mother and medium. There is no life without water."

(Albert Szent-Gyorgyi, Hungarian biochemist and Nobel Prize Winner for Medicine)

"There is no life without water, and no life in water without turbulence in water."

(Ambühl 1960)

Why is turbulence so important for plankton?

Plankton is at the base of the marine trophic web. It can be defined from a hydrodynamic point of view, as the collection of organisms that live suspended in a body of water with a limited ability to regulate its position. Therefore plankton drifts with currents, tides and other water motions, which become environmental properties inherent to planktonic life. Planktonic organisms range several orders of magnitude in size, from tenths of microns to meters, although most are microscopic. They can feed on other particles (phagotrophs) or acquire dissolved substances (osmotrophs), incorporating them into particulate form. Osmotrophic plankton dominates the flux of carbon within the pelagic ecosystem, through CO₂ fixation (primary production) and re-mineralization (respiration). In fact, the majority of primary production in aquatic systems, which accounts for roughly half of the global primary production (Field *et al.* 1998), is performed by osmotrophic plankton through photosynthesis. Parallely, bacterioplankton is responsible for the majority of organic carbon respired in the ocean (e.g. Rivkin and Legendre 2001).

The planktonic organisms capable of photosynthesizing, the aquatic equivalents of terrestrial plants, are called phytoplankton. Generally speaking, the growth of any photosynthetic organism is limited by the availability of light and/or of nutrients (the chemical elements needed for growth). This constraints the spatial distribution of primary production, because these two variables have opposite vertical distributions. Whereas light is maximal close to the surface, nutrients are almost depleted near the surface and resupply comes from the

bottom. This is particularly dramatic in aquatic systems, because light is absorbed much more rapidly in water than in air, and decays exponentially with depth, following the Beer-Lambert law.

Thus, photosynthesis in aquatic systems can take place only in a relatively thin layer, where these two oppositely distributed variables, namely light and nutrients, can coexist. The layer at which light is sufficient for photosynthesis to occur is called the euphotic zone. By the action of gravity there is a continuous flux of particulate nutrients out of the euphotic zone into the deeper layers of the aquatic systems and/or ultimately into the sediments. The vertical dimensions of oceans and seas make it impossible for phototrophic organisms, and particularly for plankton, to develop strategies for actively bringing nutrients upwards to the euphotic zone. Because planktonic organisms can not fully control their position in the water column, the whole planktonic ecosystem relies on the input of external or auxiliary energy into the euphotic zone for its maintenance (Margalef 1991). Mechanical energy input from winds, waves, tides and currents induces the mixing of the water column, and in this way brings nutrients from the deep

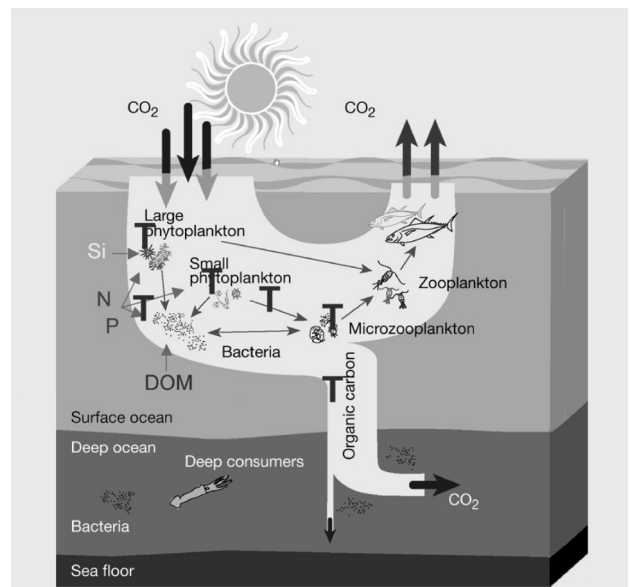


Figure 1: Schematic representation showing the main planktonic processes and fluxes influenced by small-scale turbulence in a global biogeochemical framework. Modified after Chisholm (2000).

layers or from the sediment back to the surface, where they can be utilised anew.

Turbulence is the phenomenon by which most of this mechanical energy, entered into the systems at large scales, is transferred down to scales relevant for the

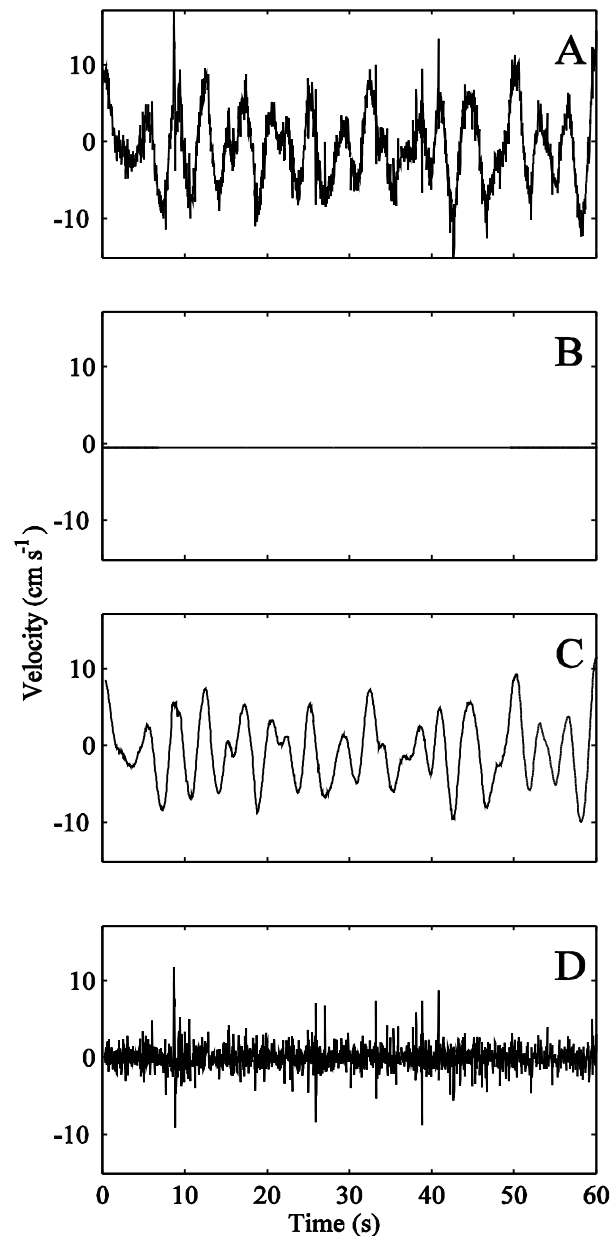


Figure 2: Decomposition of the north component water velocity signal in front of the Olympic Port in Barcelona. A, original signal, B mean intensity, C wave component, D the high frequency turbulent signal. Notice that the sum of the three signals in B, C and D results the original signal.

planktonic organisms. The study of the effects of turbulence on plankton is enormously complex, and therefore scientifically exciting. It combines the complexity of biological systems with what has been described as “the most important unsolved problem of classical physics” by Nobel prize-winner physicist Richard Feynman (1918-1988). Turbulence is an ubiquitous process with a range of temporal and spatial scales even broader than that of plankton. Consequently, its effects on planktonic organisms go well beyond the redistribution of nutrients and phytoplankton outlined above, and it affects all their processes (fig. 1). After several decades of study, we now begin to have put together pieces of the puzzle. Generally speaking, turbulence may increase the productivity of the system by increasing the efficiency of nutrient uptake by osmotrophs. It may accelerate and optimize both the input and the flux of carbon to and through the planktonic food web, and the re-mineralization of nutrients by bacteria, and can have a profound impact in the composition of the planktonic community and on its size structure. Understanding the dynamics of osmotrophic plankton and how turbulence may modulate it is important not only from a purely scientific point of view but has socio-economic implications, especially in coastal areas subjected to changing global scenarios.

Because the sources and mechanisms of turbulence generation are so diverse, turbulence is extremely variable both in space and time. It does not occur in a continuous way, but it is highly episodic, intermittent at all scales of observation. The effects of these forcings on plankton are strongly dependent on their temporal and spatial patterns, and on the ability of organisms to react to them. In the present thesis, we will deal with this variability, and with the influence it may have on coastal planktonic ecosystem dynamics, with emphasis in osmotrophic organisms, namely phytoplankton and bacteria.

A primer in turbulence

As stated by Tennekes and Lumley (1972), “in fluid dynamics laminar flow is the exception, not the rule”. Although turbulence is such a commonplace phenome-

non, ubiquitous in any fluid, it is hard to explain. Its study roots more than a century ago, but is still escaping a simple definition. To understand what turbulence is maybe the best way is to look at an example. Figure 2A shows a time series of water velocity taken in front of the Olympic Port in Barcelona. The signal can be decomposed in three different components: the trend or mean velocity (fig. 2B), the waves oscillation (fig. 2C), and an unpredictable random signal, comprising all the high-frequency oscillations (fig. 2D). The variability superimposed to the mean velocity and the wavy motions, is in fact a measure of the turbulent intensity.

According to Tennekes and Lumley (1972) a turbulent flow can be identified by being:

- **Irregular**: a turbulent flow consists of random velocity fluctuations that make a deterministic approach to its study impossible. Statistical approaches are basic tools for describing it.
- **Diffusive**: turbulence enhances the diffusion of scalar properties, such as moment, mass, heat, salinity or nutrient concentration, by several orders of magnitude. This means that it favours the flux of unequally distributed properties.
- **Dissipative**: the mechanical energy which generates turbulence is rapidly dissipated as heat at the scale of the smallest eddies. In order of a

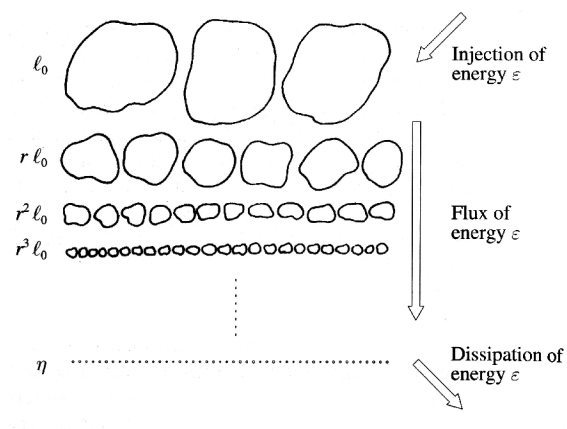


Figure 3: Conceptual sketch of the cascade of turbulence eddies according to Kolmogorov (1941). Taken from Frisch 1995.

turbulent flow to be maintained, there must be a continuous supply of energy.

- **Isotropic**: turbulence properties are equal in the three dimensions of space.

One way to identify a turbulent flow is by calculating the dimensionless Reynolds number (Re):

$$Re = \rho l u / \mu \quad (1)$$

where ρ [ML^{-3}] is the density of the fluid, l is a characteristic length scale of the motion, u [LT^{-1}] is the velocity, and μ [$ML^{-1}T^{-1}$] is the dynamic viscosity of the fluid. The Reynolds number is in fact the ratio of inertial to viscous forces. This number may be applied as well to a flow moving into a pipe and to an organism moving within the fluid. Turbulence appears at high Re , when the input of mechanical energy is large and there are strong gradients of velocity.

The cascade of energy and the turbulent scales

The transfer of turbulent kinetic energy (TKE), entered into the system at large scales, down to scales relevant for the organisms is produced through a cascade of decreasing sized eddies (fig. 3). As eddies get smaller and their Re decrease, viscosity starts to play an important role. The inertial forces are equalled by the viscosity forces at the Kolmogorov length scale (η). Below this scale eddies are no longer formed, and there remains only a laminar shear, changing randomly in direction, that dissipates heat. In the inertial subrange (from the scales of input of kinetic energy to the Kolmogorov length scale), energy is transferred at a constant rate without dissipation. Therefore, under ideal conditions, namely in isotropic, homogeneous and stationary turbulence, the rate of dissipation of turbulent kinetic energy per unit mass at the smallest scales (ϵ , [L^2T^{-3}]), must equal its rate of input at the largest scales (Taylor 1935).

The Kolmogorov length scale can be calculated as:

$$\eta = 2\pi\nu^{3/4}\varepsilon^{-1/4} \quad (2)$$

(Mann and Lazier 1989) where ν [L^2T^{-1}] is the kinematic viscosity. Typical reported values of ε for the upper ocean range between 10^{-7} and 10^{-1} cm^2s^{-3} (Mackenzie and Leggett 1993, and references therein). The η derived from these ε using equation 2 and assuming $\nu=1.047 \cdot 10^{-3}$ cm^2s^{-1} range between ca. 1 mm and a couple of cm, which are scales much larger than many of the organisms of the plankton. The Batchelor length scale (η_b) is probably more relevant in the context of osmotrophic plankton (Peters and Marrasé 2000). It refers to the smallest scale of fluctuation of scalar properties within the water, such as temperature or nutrient concentrations, due to turbulence:

$$\eta_b = 2\pi(\nu D^2 \varepsilon^{-1})^{1/4} \quad (3)$$

(Mann and Lazier 1996) where D [L^2T^{-1}] is the molecular diffusion of the scalar. η_b is lower than η , which means that although velocity fluctuations may be not perceived by most planktonic organisms, at least some will perceive the fluctuations owing to turbulence in the nutrient fields.

The maximum length scale for the largest isotropic eddies in stable stratified turbulence is known as the Ozmidov length or the buoyancy length scale:

$$l_0 = \varepsilon^{1/2} N^{-3/2} \quad (4)$$

(Denman and Gargett 1983), where N [T^{-1}] is the buoyancy (or Brunt-Väisälä) frequency, a measure of the water column stability. In the ocean, l_0 ranges between 10 cm and 100 m (Franks 2005).

Sources of turbulence in the upper ocean

Mechanical energy is entered into the system at an enormously wide range of scales (fig. 4) and by many different processes. Among these processes there is wind stress over the surface (Oakey and Elliot 1982, Oakey 1985), Langmuir circulations (D'Asaro and Dairiki 1997;

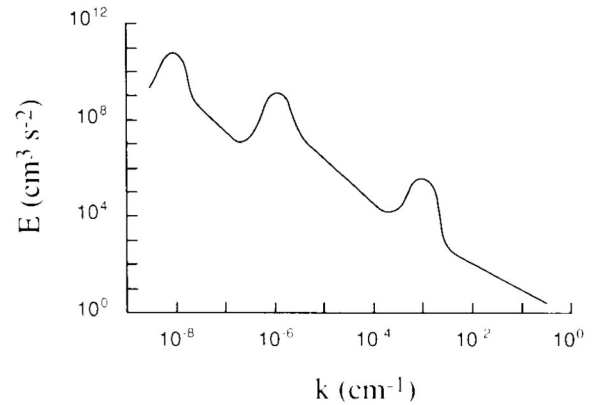


Figure 4: Distribution of energy input in the ocean for a large range of wavenumbers. Taken from Peters and Redondo 1997.

McWilliams *et al.* 1997), upwelling (Csanady 1989, Dewey and Moum 1990), tides (St. Laurent *et al.* 2002), convection (Shay and Gregg 1986) and internal waves (Sun and Kunze 1999). At the largest possible scales, energy is concentrated in quasi-stationary anisotropic cyclones and anticyclones of the order of thousands of km wide.

In the upper layer, and especially in those areas where tides are relatively unimportant (e.g. the Mediterranean Sea), wind is the dominant mechanism of energy input. The generation of turbulence by wind occurs in the first place by the stress over the water surface. According to boundary layer theory (e.g. Turner 1973, Gargett 1989), under conditions of boundary constant stress, the dissipation of energy should scale with wind speed and depth, following:

$$\varepsilon = (\rho_a \rho_w C_d^{-1})^{3/2} u_{10}^3 k^{-1} z^{-1} \quad (5)$$

(Oakey 1985), where ρ_a and ρ_w are the density of air and water respectively, C_d is the drag coefficient, u_{10} is the wind velocity at 10 m over the sea surface, k is the von Kármán's constant, typically assumed to be around 0.4 (Tennekes and Lumley 1972), and z is the depth.

In the upper layer measured dissipation rates are often higher than predicted by this model. This anomaly is attributed mainly to two wind-driven processes (Gargett

1989, Thorpe 2004): Langmuir circulations (Thorpe *et al.* 2003) and surface wave breaking (Kitaigorodskii *et al.* 1983, Agrawal *et al.* 1992, Terray *et al.* 1996, Gemmrich and Farmer 2004, Stips *et al.* 2005). This last mechanism of turbulence generation is particularly important in the uppermost layer, the wave-affected-surface-layer (WASL, Stips *et al.* 2005). In this layer, and especially in the wave-turbulent sublayer, where around half of the energy dissipation of wave breaking occurs (Terray *et al.* 1996), values of ϵ can be one or two orders of magnitude higher than those predicted by the boundary layer model (Stips *et al.* 2005 and references therein). The depth of this sublayer is estimated to be similar or lower than the significant wave height (Terray *et al.* 1996, Gemmrich and Farmer 1999), that is, than the mean height of the highest 1/3rd of the waves.

Distribution of turbulence

Turbulence is usually quantified by ϵ . Estimations of ϵ in the sea are done by means of specialized sensors, such as free-falling airfoil shear probes (Osborn 1974), and more recently by Doppler systems. Although acoustic Doppler velocimeters are becoming increasingly available to be moored for long term small-scale turbulence measurements (e.g. Gargett and Donaghay 2003) there is still a lack of data that prevents from

identifying the patterns of spatial and temporal distribution of turbulence in the sea. Measurements from free-falling microstructure profilers are scattered and since they require relatively calm sea conditions, they are also biased to low values (Peters and Marrasé 2000).

Meanwhile, in order to assess the spatial and temporal distribution of turbulence in the upper zone, it is possible to use wind data as a proxy. As we have seen, turbulence in the surface layer is mainly generated by wind driven processes, namely velocity shear, Langmuir circulations and surface wave breaking, especially in those zones where tidal flows are weak. Using data from the literature, Mackenzie and Leggett (1993) developed statistical models relating ϵ with depth and wind speed at 10 m height. These models were successfully predicting dissipation rates even in zones with tidal flows. Thus, by evaluating the temporal and spatial distribution of wind from easily available meteorological time series, it is possible to assess the distribution of turbulence events in the upper ocean.

Effects of turbulence on plankton

Scales of interaction

Since turbulence is a multi-scaled process, its influence on planktonic organisms operates at very different spatial and temporal scales. Essentially, effects of turbulence can be classified between those at the large scales and those at the small scales (Thomas *et al.* 1997). At the large scales turbulence affects the relative distribution of plankton and its resources, namely light, nutrients and prey. At the small scales, turbulence tends to accelerate the energy and matter transfer processes through the planktonic food webs (Peters and Marrasé 2000).

Large scales: redistribution of plankton and resources

The external mechanical energy entered into the system has an important seasonal component in temperate waters. It is usually maximum in autumn and winter and minimum in summer. This determines

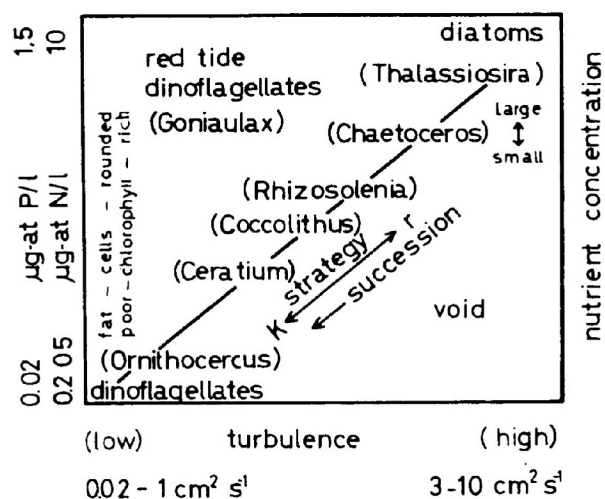


Figure 5: Original Mandala of Margalef (1978). Planktonic organism placement in a two-dimensional space of nutrient concentration and external energy

seasonal patterns in the phytoplanktonic succession, elegantly summarized in “Margalef’s mandala” (Margalef 1978, Margalef *et al.* 1979). In this two-dimensional ecological space (fig. 5), defined by the input of nutrients and by turbulence intensity, different phytoplanktonic life-forms are distributed following the common seasonal succession in temperate waters, from low turbulence-low nutrients to high turbulence-high nutrients conditions. Diatoms, a group of non-motile unicellular algae, are dominant in winter, when the water column is well mixed and nutrient concentrations are relatively high. In late winter or early spring, as solar irradiance increases, water column is stabilized by thermal stratification. During a short period, nutrient concentrations in the surface layer are still high as a result of the winter mixing, and light is non-limiting. In these conditions the annual maximum in biomass is achieved, due mainly to diatoms. It is the spring or late-winter bloom (Sverdrup 1953). Ultimately, nutrients are depleted from the euphotic zone. In summer the phytoplanktonic community is dominated by motile forms like dinoflagellates, and small algae like cyanobacteria. This seasonal cycle is restarted again in autumn, when low solar irradiance weakens the thermocline, and strong winds and waves deepen the mixed layer.

Situations with low-turbulence and high-nutrient concentrations are anomalous, and may conduct to blooms of dinoflagellates, the so called red tides. Several dinoflagellates life-form species (as defined by Smayda 2002) may however bloom also under turbulent conditions, namely in fronts or upwellings, taking advantage of their swimming capability to counteract dispersion and sinking (Smayda 2002).

Thus, the occurrence of turbulence is often associated to increased nutrient concentrations (Margalef *et al.* 1979). Nutrients are the chemical elements of which organic matter is made of, and are thereby essential for the growth of organisms. The most ecologically important nutrients in aquatic systems are N, P, Si and Fe, because they are the ones most frequently found in limiting concentrations for phytoplankton growth. Redfield (1934) proposed that the ratios between the concentrations of these elements in deep waters were

reflecting the ratios within the planktonic organisms in the euphotic zone. The so called Redfield atomic ratio is C:Si:N:P= 106:15:16:1 (Redfield *et al.* 1963). Deviations from this ratio in the organic matter or in the ambient water are generally thought to be symptomatic of limiting growth conditions for plankton.

Once nutrients have been incorporated into the particulate fraction they tend to sink downwards. The velocity of this flux will depend on the size structure of the planktonic community and on the recycling processes within the water column, but it is a general trend, even for the smallest organisms (Richardson and Jackson 2007). Ultimately, in order to sustain new production

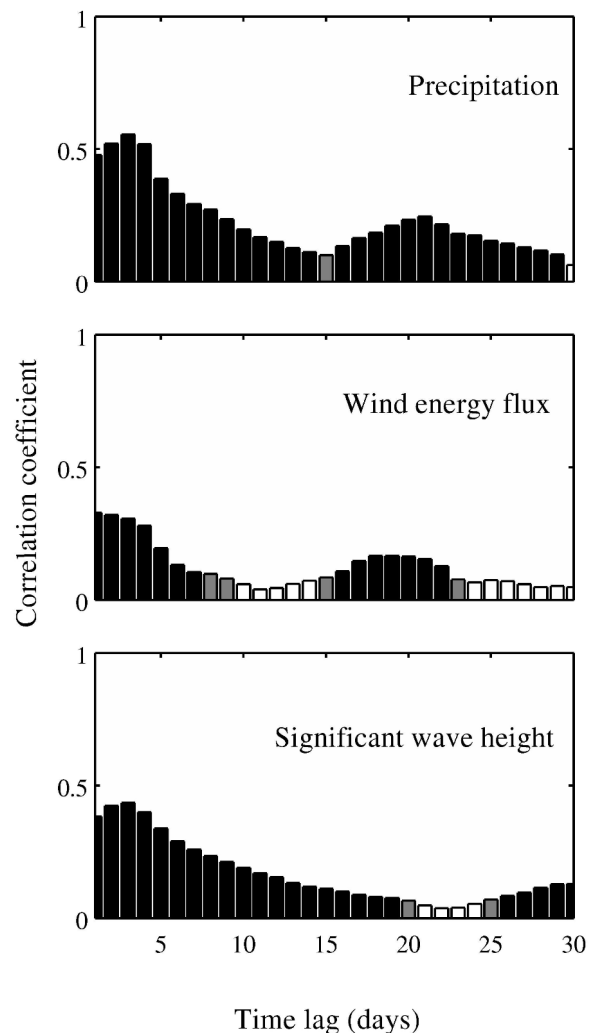


Figure 6: Cross-correlograms between La Tordera river discharge, and precipitation, wind energy flux and significant wave height. Details of calculation are given in chapter 3.

there has to be a replenishment of inorganic nutrients to the euphotic zone. The supply of nutrients to the surface is due to atmospheric deposition, terrestrial runoff and the input from the bottom.

The open sea template

In deep waters, turbulence can decrease water column stability and eventually disrupt the thermocline. By deepening the mixed layer and/or increasing the turbulent flux through the thermocline, it can bring up bottom waters rich in nutrients or in seeding diatoms (Smetacek 1985). Besides, turbulence changes the light climate of the phytoplankton in two senses. In the first place it increases the variability of light at which cells are subjected (Denman and Gargett 1983), which may favour again the dominance of diatoms, because these are well adapted to fluctuating light regimes (Litchman 2000). In the second place, whenever it causes the deepening of the mixed layer it decreases the average amount of light each cell receives. If the mixing layer is too deep, the photosynthesis performed in the euphotic zone may not compensate for the respiration occurring throughout the mixed layer. The depth at which integrated production and respiration are equal is called the critical depth (Sverdrup 1953, Mann and Lazier 1996, Huisman *et al.* 1999). If mixed layer depth is below this critical value, the integrated respiration through the mixed layer is higher than the production, and therefore phytoplankton can not have a net growth.

However, the existence of a mixed layer is not a *sine qua non* for the development of phytoplankton blooms in deep waters. If turbulence is below a critical maximal value, even in the absence of a mixed layer or when this is deeper than the critical depth, the growth rate of phytoplankton in the euphotic zone may exceed the vertical mixing rates (Huisman *et al.* 1999, 2002). In addition, turbulence must be above a minimal turbulence intensity to neutralize the loss due to sinking (Huisman *et al.* 2002).

Coastal areas

In shallow systems, as for example in coastal waters or small lakes, turbulence may resupply nutrients from bottom layers by directly increasing the flux of nutrients from the sediment (Dade 1993, Grémare *et al.* 2003). Another major source of nutrients in coastal zones is the terrestrial runoff. In the past decades there has been an anthropogenic worldwide tendency to increase the concentrations of nutrients in freshwater inputs (Cloern 2001). The temporal dynamics of terrestrial input, especially in a dry climate as the Mediterranean, is linked to the meteorological forcing variability (fig. 6). Thus, the nutrient input from rivers and ephemeral water courses has a strong episodic component in the Mediterranean coasts, which is also related to the pattern of turbulent events.

The turbulence-driven resuspension of sediments, besides increasing the concentration of nutrients in the water column, can lead to increased turbidities and consequently to a limitation of the light available for photosynthesis (Cloern 1987, Cotner *et al.* 2000). Thus, the response of coastal phytoplankton to mixing episodes may be not immediate. A lag, related to the time for the large suspended material to sink again, may exist between the beginning of the perturbation and the observed increase in production.

Effects on the spatial distribution of scalars

Planktonic organisms do not distribute uniformly. Their distribution depends on food, nutrient and light fields, on biological processes, such as growth or predation, and on water motion. The influence of turbulent motions in the spatial distribution of planktonic organisms may be seen from spectral analysis. In Fourier or spectral analyses a data series is decomposed in sines and cosines functions with increasing wave numbers. The amplitude of a given function depends on the variability (or energy) associated to its wave number. In turbulence, the energy (E) spectrum in the inertial subrange follows:

$$E(k) \propto \varepsilon^{2/3} k^{-5/3} \quad (6)$$

(Kolmogorov 1941), where k is the wave number. Scalar properties, such as temperature or salinity, show a variance spectrum with the same slope than turbulence, $-5/3$, because they behave almost as passive tracers of the water motion (Batchelor 1959).

Nutrient concentrations and fluorescence, a proxy for the chlorophyll concentration and therefore for the phytoplankton biomass, have also been reported to follow the $-5/3$ law within the inertial subrange in numerous situations (Platt 1972, Yamazaki *et al.* 2006, Mountain and Taylor 1996). This suggests that to some extent they behave also like passive tracers (Denman and Platt 1976). At the largest scales, above the Ozmidov length scale, the distribution of plankton is dominated by biological processes, like growth or grazing, and slope is theoretically closer to -1 (Franks 2005). Below the Batchelor scale, at the smallest viscous scales the slope is also close to -1 . But at the inertial subrange the slope may approach to $-5/3$. Recently Franks (2005) has pointed out the severe methodological artefacts that this kind of studies often suffers from. Among them, sampling with frequency out of the inertial subrange and assuming plankton to be a continuum variable, rather than quanta. Still, the spectrum of plankton has been seen to follow a $-5/3$ slope under strong turbulent conditions, when inertial subrange is broader, suggesting the importance of turbulence in the distribution of plankton and nutrients (e.g. Mountain and Taylor 1996). Deviations from the $-5/3$ theoretical slope within this range may occur because of interactions between plankton populations (Powell and Okubo 1994). Besides, many organisms have motility, or at least have densities higher than seawater (Ghosal *et al.* 2000), and therefore their movement is not completely solidary with water motion, departing from being perfect tracers.

Large scale turbulence can also dissipate patches or layers of elevated food concentration, hence affecting food availability to planktivorous predators (Kjørboe 1997). In addition, turbulence may affect the distribution of vertical migrating organisms by disturbing their swimming behaviours or patterns (Kamykowski 1995).

Small scales: effects on individuals

Effects of turbulence at the small scales are related to the turbulent motion *per se*, but also to the laminar shear field which derives from this motion and which is found below the Kolmogorov microscale. At these small scales and below, the direct effects on individuals are basically caused by an increased flux of solutes or particles to the organisms. This simple statement translates into different effects, depending on the trophic behaviour of the organism, and on its size. For osmotrophic cells small-scale turbulence leads to an enhancement of uptake rates of nutrients (Karp-Boss *et al.* 1996). For phagotrophic organisms, it means an increase in encounter rates between particles (Rothschild and Osborn 1988), which has implications in grazing, mating and aggregation. At these small scales turbulence has also been seen to increase sedimentation velocities (Ruiz *et al.* 2004). Finally, turbulence has been reported to inhibit cell processes at the ecophysiological level (Berdalet 1992), particularly in dinoflagellates.

Uptake of nutrients and cell size

The flow of solutes to and from a cell is ultimately controlled by molecular diffusion. At the steady state, and in the absence of relative fluid motion, the diffusional flux Q of a solute with molecular diffusion coefficient D [L^2T^{-1}] into an ideal spherical cell of radius r_0 can be described by:

$$Q = -4\pi D r_0 (C_\infty - C_0) \quad (7)$$

where C_∞ and C_0 are the ambient and cell surface concentration of the solute respectively.

According to Kjørboe (1993) the volume specific uptake rate Q' scales with the minus 2nd power of radius:

$$Q' = \frac{Q}{4/3\pi r_0^3} = -3 D r_0^{-2} (C_\infty - C_0) \quad (8)$$

This means that small cells are more efficient in taking up or releasing solutes than large cells. The latter

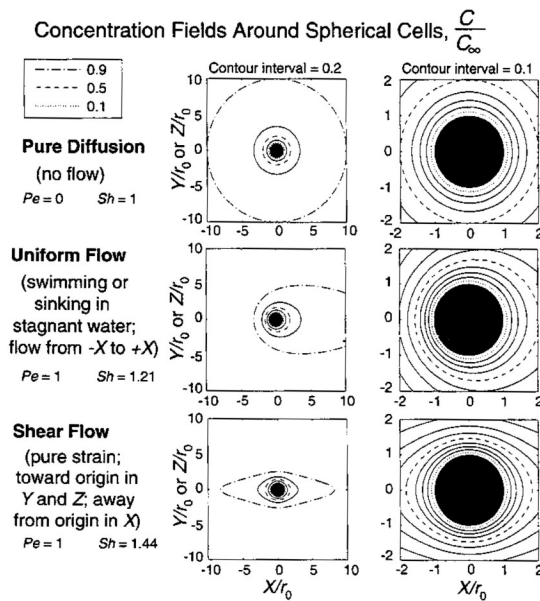


Figure 7: Solute concentration fields around idealized spherical cells, standardized to surface concentration, under three different flow regimes: still water, laminar flow derived from sinking or swimming and small scale shear occurring under turbulent conditions. Taken from Karp-Boss *et al.* 1996.

can easily become diffusion limited, and are at disadvantage in oligotrophic waters.

On the other hand the optimal cell size increases with increasing nutrient concentration (Jumars 1993, Jumars *et al.* 1993, Karp-Boss *et al.* 1996). According to these authors, the gross loss of substrate scales with mr_0^2 , where m is a coefficient for catabolism of the cell. The optimal cell size r_{opt} is achieved when the difference between uptake and loss is maximum, i.e., when:

$$\frac{d(4\pi r_0 D(C_\infty - C_0) - mr_0^2)}{dr_0} = 0 \quad (9)$$

which gives:

$$r_{opt} = \frac{2\pi D(C_\infty - C_0)}{m} \quad (10)$$

Thus, optimal cell size is directly related to the diffusion coefficient and to the ambient concentration, which may explain why large cells are more common

under eutrophic conditions. The availability of nutrients is therefore partly determining the size structure of the osmotrophic community. Diatoms may partly escape this general relationship, because they have a big vacuole inside, which lower their requirement in nutrients with respect of what would be expected for their size.

Although, as stated above, molecular diffusion controls the uptake of nutrients, turbulence derived laminar shear, as well as relative fluid motion in sinking and swimming cells, can indirectly increase the flux of solutes by steeping their concentration gradient and thus thinning the boundary diffusional layer (fig. 7). The increase in nutrient uptake due to fluid motion will depend in general of three variables: the flow regime (laminar shear, turbulent or laminar motion), the size and shape of the cells, and the diffusion coefficient D of the solute (Karp-Boss *et al.* 1996). For the range of turbulence levels encountered in the ocean surface, the relative increase in uptake rate of dissolved inorganic nutrients due to fluid motion is important only for microphytoplankton (cell sizes between 20 and 200 μm).

Thus both high nutrient concentration and vigorous turbulence flows are in general relatively favouring large cells or chains, although this is probably not enough to counterbalance the advantage in nutrient uptake of being small, and can not explain by itself the dominance of large cells in the phytoplanktonic community at certain times of the year (Kjørboe 1993).

Encounter rates

Small scale turbulence increases the encounter probability rates between particles because it increases the relative velocity between them. This was first envisioned by Rothschild and Osborn (1988) dealing with predator-prey contact rates. Under moderate turbulence levels this enhancement may translate into higher grazing rates, but this will depend on the size (and velocity) of both predator and prey, and especially on their behaviour. Under strong turbulence these positive effects can be in part counterbalanced by higher energy expenditure, related for example with escape responses (Marrasé *et al.* 1990), and by lower capture efficiency (Saiz and Kjørboe

1995, Mackenzie and Kiørboe 2000). In the case of feeding rates therefore, the effect of turbulence is dome-shaped, being maximal at intermediate levels of dissipation.

The theoretical positive effect is most important for predators of sizes near the Kolmogorov length scale, such as copepods and fish larvae (Kiørboe and Saiz 1995, Kiørboe 1997). Turbulence has been experimentally seen to enhance encounter and feeding rates for both copepods (Marrasé *et al.* 1990, Saiz *et al.* 1992, Saiz and Kiørboe 1995) and fish larvae (Sundby and Fossum 1990, Sundby *et al.* 1994). For much larger organisms the turbulent velocity is too slow to be of any significance when compared with the organism velocity. Below the Kolmogorov scale the laminar shear can also create relative motion between protozoan predators and their prey. Several experimental responses of protozoan grazing rates to small-scale turbulence or laminar shear have been reported (Peters and Gross 1994, Shimeta *et al.* 1995). Thus, turbulence may accelerate carbon transfer rates within the microbial food web.

Another consequence of the increase in contact rates is the enhancement of the coagulation of particles (Jackson 1990, Kiørboe 1994, Kiørboe 1997). Aggregation is responsible for the formation of the marine snow. The increased coagulation leads to higher settling velocities (Kiørboe 1997).

Physiological effects: the case of dinoflagellates

The response of the different planktonic groups to small-scale turbulence is very diverse, not only because of size-dependent dynamics and differences in life styles and morphologies, but also because of physiological effects. Thomas *et al.* (1997) predicted the sensitivity to turbulence in phytoplankton groups to order as follows: chlorophytes < cyanophytes < diatoms < dinoflagellates.

Dinoflagellates constitute the group of algae most sensitive to turbulence, and which has been more extensively studied under this point of view. This conclusion derives from both field observations and experimental studies. Dinoflagellates blooms are most

usually favoured by periods of calm weather conditions and high water column stability (Wyatt and Horwood 1973, Margalef 1978, Berman and Shteiman 1998). Numerous experimental studies have addressed the particular responses to turbulence of dinoflagellates (for a review see for example Estrada and Berdalet 1997, 1998, Thomas *et al.* 1997, Berdalet and Estrada 2005), which appear to be highly species-specific (Berdalet and Estrada 1993, Sullivan and Swift 2003, Berdalet *et al.* in press). Although the growth of some species is insensitive to or favoured by small-scale turbulence, a diversity of negative effects have reported including inhibition or even suppression of net growth (Berdalet 1992, Thomas and Gibson 1992, Berdalet and Estrada 1993), inhibition of cell division (Berdalet 1992, Thomas *et al.* 1995), induction of changes in cell morphology (Zirbel *et al.* 2000), loss of flagella (Thomas and Gibson 1990), or alteration of the swimming behaviour (Pollinger and Zemel 1981, Thomas and Gibson 1990, Zirbel *et al.* 2000, Berdalet *et al.* in press).

The ecological relevance of the sensitivity of dinoflagellates to turbulence remains to be tested in some aspects. In the field diatoms are generally in a competitive advantage over dinoflagellates under mixing conditions. Diatoms and dinoflagellates probably represent two opposite evolutionary strategies to the problem of diffusive limitation of the uptake of nutrients in large osmotrophic cells. While dinoflagellates increase the uptake rates by actively swimming, diatoms take advantage of turbulent motion as well as of high sinking speeds and changing buoyancy.

Ecosystem effects

The study of the effects of turbulence at an ecosystem scale has been based mainly on enclosure experiments with natural planktonic assemblages (e.g. Reynolds *et al.* 1983, Oviatt *et al.* 1981, Estrada *et al.* 1987, 1988, Howarth *et al.* 1993, Peters *et al.* 1998, 2002, Petersen *et al.* 1998, Svensen *et al.* 2001) because it is easier to separate the effects of turbulence from those of other environmental factors. Several robust trends arise from such studies, which confirm most of the theoretical and physiological effects outlined in previous sections.

Changes in community composition

Margalef's Mandala (fig. 5), which is mainly based on field observations, has been confirmed by numerous enclosure studies. Several investigations have shown that turbulence, especially when in conjunction with nutrient enrichment, increases the proportion of diatoms (Oviatt 1981, Reynolds *et al.* 1983, Estrada *et al.* 1988, Petersen *et al.* 1998, Arin *et al.* 2002). By contrast, flagellate and small forms are dominant under still conditions or at mature stages of the succession (Estrada *et al.* 1987). Some of the variability in the community response to perturbations is undoubtedly caused by differences in the initial community composition (Estrada *et al.* 1987).

Although turbulence increases encounter rates, this does not necessarily translate into higher growth rates of consumers. In fact, in turbulent microcosm experiments with the natural community, copepods are often in lower abundances (Oviatt 1981, Alcaraz *et al.* 1988, Petersen *et al.* 1998). At high levels, turbulence increases metabolic rates and reduces feeding efficiency by disturbing feeding currents or enhancing escape reactions.

Size structure

The slope of the biomass-size spectrum may be smoothed by the influence of turbulence (Arin *et al.* 2002, Cózar and Echevarría 2005) and of nutrient enrichment (e.g. Duarte *et al.* 2000, Samuelsson *et al.* 2002, Malits *et al.* 2004). Episodic nutrient input and turbulence are predicted to cause the dominance of microphytoplankton for two reasons: because these conditions favour the uptake of nutrients by large cells (bottom-up effect), and because small cells can not fully respond to these inputs because of a tighter control by their predators (top-down effect).

This top-down effect deserves some development. All specific metabolic rates, as for example growth, scale with body size following:

$$M \propto V^b \quad (11)$$

where V is the organism volume and b is an exponent which is remarkably close to $-1/4$ for both unicellular and multicellular organisms (Banavar *et al.* 2002). That is, small organisms are more rapidly growing. The size ratio between predator and prey is fairly constant, between 10:1 and 100:1 (Kiørboe 1993 and references therein). The generation time scales with the inverse of the growth rate. The difference in generation times between prey and predator, and therefore the response time of grazers, tends to get longer the larger the organisms. As a consequence, the top-down control is stronger over small osmotrophic cells than over large ones (Kiørboe 1993, Franks 2001). Whereas any increase in growth of small cells will be quickly matched by growth in their predators, large cells are more likely to grow unchecked and to eventually result in a bloom.

Episodic inputs of nutrients and/or of external energy trigger phytoplankton growth, and especially large phytoplankton growth. As episodes are limited in time, it is possible that large consumers are not able to respond to them. Thus, episodes can potentially uncouple different parts of the planktonic food web, particularly large producers from large consumers. This may lead for example to the formation of diatom blooms which settle out to the bottom, eventually producing episodes of net carbon export and sequestration (Kiørboe 1993). The duration and frequency of such episodes will ultimately determine the possibility of mesozooplankton (zooplankton between 200 μm and 2 cm) to respond to the increases in microphytoplankton. If events are long and intense enough to produce phytoplankton response, but too short to allow zooplankton to react, likely there will be a bloom. This situation may be maximized if copepods, which constitute the main group of mesozooplankton, are negatively affected by turbulence rather than being favoured by higher encounter rates.

The smoother the size spectrum, the shorter the food chain, and the more efficient the transfer of energy and matter to the highest trophic levels, namely fishes. In other words, the classical food web should be relatively more important after events of nutrient enrichment and turbulence. This is important for two reasons: the

production of pelagic fishes may be higher, and the sequestration of organic carbon may also be higher.

Metabolic and stoichiometric changes

Both phytoplankton and bacteria need inorganic nutrients for their growth. This can potentially lead to situations of competition between them (Bratbak and Thingstad 1985, Thingstad *et al.* 1993, Thingstad and Rassoulzadegan 1995). Theoretically, because of the strong size-dependence of the effects of turbulence and nutrient fertilization, it is expected that both factors, especially when occurring together, will relatively favour the dominance of phytoplankton, and particularly of diatoms, over bacteria (Maar *et al.* 2002). Thus, the fraction of osmotrophic biomass which is heterotrophic should decrease under eutrophic and turbulent conditions, that is, the importance of the microbial loop (Pomeroy 1974, Azam *et al.* 1983) is expected to be smaller. Turbulence is predicted to be a potential modulator of the degree of autotrophy of planktonic community. Furthermore, its observed effects on natural populations of copepods (e.g. Alcaraz *et al.* 1988, Petersen *et al.* 1998) may increase this tendency. Again, this has implications on the export and sequestration of C (Legendre and Le Fèvre 1989, Thingstad and Rassoulzadegan 1995) as well as on the production of pelagic fishes (Kiørboe 1993).

After a strong nutrient input event turbulence pushes the system to relatively more autotrophic conditions (Alcaraz *et al.* 2002, Arin *et al.* 2002, Maar *et al.* 2002), by enhancing the growth of phytoplankton, particularly diatoms (Reynolds *et al.* 1983, Estrada *et al.* 1987, Petersen *et al.* 1998, Oviatt *et al.* 1981, Arin *et al.* 2002). Alcaraz *et al.* (2002) found the system to be kept net autotrophic longer in turbulent treatments, although both primary production and respiration were higher under turbulent conditions.

In stronger nutrient limiting situations, by contrast, turbulence relatively increases the percentage of heterotrophic biomass (Peters *et al.* 1998, 2002). This increase is due mainly to positive responses of bacteria. Bacteria are theoretically too small to benefit from

increased inorganic nutrient uptake rates (Karp-Boss *et al.* 1996), and generally do not respond to natural levels of turbulence neither in cultures nor in predator-free environments (Moeseneder and Herndl 1995, Peters *et al.* 1998, 2002, Malits *et al.* 2004). However, turbulent flow may significantly increase the uptake of high-molecular-weight dissolved molecules and directly induce changes in the size-structure of the bacterioplankton community (Malits *et al.* 2004). The increase in bacterial abundance under natural turbulent conditions often happens only when the whole microbial food web is present. It has been hypothesized that the cause is a release in the grazing pressure over bacteria as heterotrophic flagellates can change to larger and more nutritious prey, namely pico- and nanophytoplankton (Peters *et al.* 1998, 2002). The described changes in the composition and size structure of the community lead to an increase in the total amount of particulate organic carbon (Peters *et al.* 2002) and to changes of the stoichiometric ratios (C:N:P) of the particulate organic matter (Maar *et al.* 2002).

Thus, turbulence episodes would at first either enhance the autotrophic component of the community or favour the microbial loop and accelerate the recycling of nutrients, depending on the nutrient input associated to the episode. The situation of high-turbulence-low nutrients is considered as void space in Margalef's Mandala of phytoplankton (fig. 5). ¿Could it be a heterotrophic space dominated by bacteria and small phytoplankton?

Sedimentation

The common impression is that turbulence keeps particles in suspension. This seems to be a fact in shallow waters (a coastal bay, a cup of coffee), where turbulent mixing resuspends particles from the bottom (Garstecki *et al.* 2002). However there is still some controversy about the effects of turbulence on sedimentation of particles in deep waters. Recent experimental work (Ruiz *et al.* 2004) points that, contrary to intuition, small-scale turbulence increases the sedimentation velocities of particles denser than water. Models suggest that when taking into account the whole mixed layer, with

decreasing dissipations with depth, turbulence may decrease the sedimentation velocity of phytoplankton cells by altering their vertical distribution (Ruiz 1996, Ruiz *et al.* 1996, Ross 2006). This effect will be more important for fast sinking particles, and will depend therefore on the size structure of the community and on the physiological state of the different populations (Ruiz *et al.* 1996). However, a thorough understanding of the interaction of turbulence with settling particles is still lacking.

Besides its direct influence on sedimentation velocities of particles, turbulence is going to indirectly affect the downward flux by changing the size structure of seston (particles in suspension, both life and dead). As seen above, turbulence promotes the growth of larger and non-motile fast sinking cells and the transfer of matter up in the food chain through enhanced grazing rates. It also increases aggregation between particles (Kiørboe 1997). The sinking velocity of particles is in direct relation with the radius of the particles according to the Stokes' law. Therefore, *a priori* larger particles means higher sedimentation rates.

In summary, turbulence may increase the flux of dissolved to particulate material, and at the same time the velocity with which this material sinks out of the mixed layer. Episodic turbulence events may therefore not only stimulate the growth of phytoplankton, but also cause a large part of the newly produced organic matter to be exported out of the euphotic zone by sedimentation. As dynamics of episodes is strongly linked to global change patterns (IPCC 2007), their understanding is crucial to comprehend biogeochemical cycle.

Variability of turbulence

The spatial and temporal variability of turbulence is key to understand the effects of mixing on planktonic ecosystems, as well as on the distribution of planktonic organisms. In the temporal domain, for example, frequency, intensity and persistence of turbulence episodes (above a certain background level) must be taken into account. The frequency of episodes is going to determine the ability of the planktonic community to

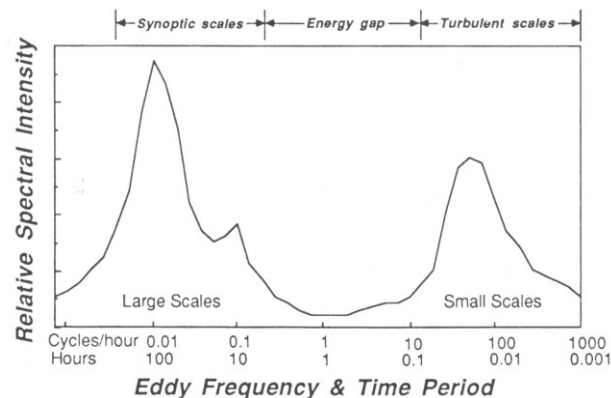


Figure 8: Schematic spectrum of wind speed near the ground. Note that most of the wind energy is concentrated in the synoptic scales, in the range of hours and days. Taken from Stull 1988.

adapt to them, and may thus shape the community in the long run. The intensity will determine which organisms and processes will be affected by the episode, according to size and specific sensitivity. Finally the persistence of the episode will determine the fate of the carbon produced, because it may explain decouplings between different groups of the trophic web, for example between diatoms and copepods.

We have had a quick look at the wide range of scales at which turbulence may affect planktonic processes. It is important to understand that turbulence is intermittently distributed at all these scales both in the spatial and temporal domains (e.g. Jiménez 1997, Jou 1997). At the smallest scales (s, cm), it is also intermittently distributed into tiny bursts or patches. The temporal variability at the smallest scales (in the order of seconds) must be compared with physiological and behavioural processes, such as nutrient uptake, production or prey capture rates. From the point of view of planktonic organisms, it may be understood as a “hydrodynamic weather” (Catalan 1999). The topic of the distribution of turbulence at these smallest scales, and of its effects on plankton, is most interesting but out of the scope of the present thesis.

We have based our research on the topic of larger scale variability (hours to days, metres to decametres), the “hydrodynamic climate” (Catalan 1999). At these scales, the distribution of turbulence is linked to the

variability of the forcing parameters, such as wind (fig. 8). Most of the energy entered into the system from winds is concentrated in the range between hours to days, which is also in the range of demographic rates, such as growth and grazing that can be studied through changes in biomass. Episodic events of turbulence and the related nutrients inputs are perturbations of the planktonic ecosystem. As their time ranges are so close to the generation times of planktonic organisms, they may continually keep the ecosystem from reaching an equilibrium and may help explain the high diversity of planktonic organisms (Hutchinson 1961, Kemp and Mitsch 1979).

Few studies have approached experimentally the topic of temporal variability in turbulence and nutrient input. Eppley *et al.* (1978) mixed large experimental enclosures (1700m³) daily and found that diatom chains >100µm were dominant throughout the experiment, whereas in unstirred treatments small flagellates became more important at the end of the experiment. Estrada *et al.* (1988) subjected natural planktonic assemblages to nutrient fertilization and vigorous mixing with a periodicity of 2-3 days. They found that the system responded with fluctuations at frequencies lower than those of forcing. This is, according to these authors, a typical feature of non-linear systems. Alcaraz *et al.* (2002) subjected 15 L enclosures to three levels of turbulence: non-turbulent, continuously turbulent ($\epsilon=0.05 \text{ cm}^2\text{s}^{-3}$), and intermittent (2 days still, 2 days at $\epsilon=0.10 \text{ cm}^2\text{s}^{-3}$). They found changes in the metabolism and trophic status of enclosures due to the mode of input. Intermittent turbulent enclosures were found to keep autotrophy for a longer time.

Other ecophysiological studies, focused mainly on red-tide forming dinoflagellates, have studied the responses of several species to temporal intermittent laminar shear flows using Couette devices (Gibson and Thomas 1995, Juhl *et al.* 2000, 2001, Juhl and Latz 2002). Gibson and Thomas (1995) reported that a brief daily exposure to high turbulent shear is enough to inhibit the growth of these organisms. Other studies (Juhl *et al.* 2000, 2001, Juhl and Latz 2002) have shown that the sensitivity of dinoflagellates to turbulent flow

depends on the growth phase of the culture, i.e. on its physiological state, and on the frequency and persistence of exposure. Thus, the duration and frequency of the turbulence events in the case of dinoflagellates seems to be important. Often times, cells will not divide until calm conditions are re-established (Berdalet 1992, Berdalet *et al.* 2007).

Study of turbulence effects on plankton: experimental vs. field work?

The study of the influence of turbulence on planktonic organisms faces several methodological constraints. Most hypotheses, especially those concerning small-scale turbulence, are very difficult to test in the field. In the first place, because there are many other co-varying parameters, some of them with a strong effect in plankton (e.g. light or temperature or nutrients), which can obscure the effects of turbulence. Besides, organisms are advected with the water and it is difficult to track the changes of a particular water mass. Finally, turbulence is highly intermittent in time and space and at very different scales of observation. In summary, the system has many degrees of freedom. Field studies therefore must rely on joint statistical analyses of biological parameters under a range of different hydrodynamic situations (Pollinger and Zemel 1981, Haury *et al.* 1990, 1992, Sundby and Fossum 1990, Irigoien *et al.* 2000). These studies have the advantage of looking at the integrated effect of turbulence on the ecosystem, although robust conclusions may be difficult to draw because of the number of parameters playing a part.

Traditionally, the effects of turbulence have been studied in controlled enclosures. This eliminates the problem of advective changes, and allows a tighter control of environmental conditions, like temperature light or other. The possibilities to test hypotheses, to find cause-effect relationships and to take advantage of replication to increase statistical power, are all characteristics of enclosure experiments. The drawback is that the results obtained can not be easily extrapolated to the field. In addition to the methodological artifacts associated with placing organisms in closed systems,

such as uncontrolled changes in behaviour, in community composition, or in growth dynamics, we face the challenge of generating realistic turbulence, both quantitatively and qualitatively. More in depth treatments of the topic of generating turbulence in experimental containers can be found in Peters *et al.* (1997) and Sanford (1997).

One of the main problems is that the spatial scales of energy input and generation of turbulent motions are much larger in the sea than in the largest experimental enclosures. This limits the possibility to assay the effects of large scale mixing, because a whole turbulent cascade is not possible. However, several experimental systems have successfully reproduced some aspects of the vertical structure of the water column, like the pycnocline (e.g. Donaghay and Klos 1985, Estrada *et al.* 1987). Other studies have focused on the simulation of fluctuating light conditions as those experienced by phytoplankton under different mixed layer depths and turbulent intensities (e.g. Marra, 1978, Litchman 1998).

Enclosures with stirring are better suited for studying the effects of small-scale turbulence. At these scales characteristics of turbulence are more independent on the mechanism of generation (Sanford 1997), and they tend to be approximately isotropic, that is, equal in all spatial directions. However, to our knowledge no one has really tested the degree of isotropy in most experimental systems. The quantification of small-scale turbulence levels has been a major problem in microcosm experiments. In the first place, it is not clear what physical parameter (if any) is the best descriptor of the turbulence as experienced by planktonic organisms. The parameters used most often have been the turbulent kinetic energy dissipation rate, the shear rate (or the strain rate) and the turbulent diffusivity. Second, the measurement of flow velocities in the containers, especially when these are small, is difficult, because it requires of specialized, and often customized, technology. As a consequence the determination of turbulence in experimental enclosures, if done, has been performed with a diversity of sensors and methodologies, or using different theoretical models. This poses a

difficulty when comparing different studies between them, or with field conditions.

The experimental devices used to study turbulence are many. Among them the most popular in ecological research are oscillating-grid or oscillating-rod systems (e.g. Hopfinger and Toly 1975, Estrada *et al.* 1987, Peters *et al.* 2002), shaker tables (e.g. Berdalet 1992, Saiz and Alcaraz 1992, Colomer *et al.* 2005, NRC 2005), bubbling (e.g. Eppley *et al.* 1978, Estrada *et al.* 1988), paddles (e.g. Donaghay and Klos 1985), etc... Couette cylinders have been used extensively to study the response of organisms, particularly of dinoflagellates, to laminar shear (e.g. Thomas and Gibson 1990, 1992, Thomas *et al.* 1995, Juhl *et al.* 2000, 2001, Karp-boss *et al.* 2000, Juhl and Latz 2002).

The turbulence levels used in these studies have often been high and even unrealistic. In recent years the trend in this kind of experiments has been to lower the turbulence levels in order to approach experimental conditions to nature. A next step in this direction must be to shorten the duration of experiments, or to reproduce a temporal pattern of energy intensity, because in the field turbulent events are episodic, limited in space and time. Therefore, effects on the enclosed natural community of strong turbulence after several days of treatment are hardly generalisable to the field. The problem lies in that, although the database of turbulence measurements in the field is continuously increasing, to our knowledge there has not been any systematic study addressing the temporal or spatial distribution of turbulence. In addition, as previously mentioned, this dataset is likely biased towards low levels (Peters and Redondo 1997), because sampling and measuring under strong turbulent conditions from a ship is difficult. With the mooring of high frequency physical and biological probes, this lack of data will disappear, at least for coastal areas. This will allow deriving robust conclusions from field data and keeping refining ecologically relevant experiments.

Aims and outline of this thesis

Episodic inputs of turbulence, often associated to nutrient inputs, stimulate the growth of large non-motile

phytoplankton cells (basically diatoms) and their aggregation, leading to events of carbon export. Our present knowledge of the temporal and spatial distribution of turbulence in the euphotic zone at a synoptic scale, and on the overall effects of this variability on planktonic systems is very scarce. In addition, both the nutrient load to coastal zones and the frequency and intensity of turbulence events are subject to global changes.

The overall aim of the present thesis is:

To address how the variability in forcing factors, especially turbulence, affects the dynamics of coastal plankton communities.

We have approached the problem from different points of view and using different techniques, always trying to link field data with laboratory experiments. We have used meteorological time series of winds to assess the spatial and temporal distribution of wind events in the surface waters of the Catalan (NW Mediterranean) coast (chapter 1). As a mean to improve our interpretation of laboratory generated data we have we have characterized, both qualitatively and quantitatively, the turbulence generated in two of the most common devices used in the laboratory: oscillating grids and shaker tables (chapter 2). In chapter 3 we present the results of a time series study, in which we have linked the size structure and composition of the osmotrophic planktonic community in Blanes Bay to the episodic inputs of nutrients and external energy. In chapter 4 we evaluate the sensitivity of the osmotrophic planktonic community, throughout a whole year, to simulated nutrient load and turbulence episodes by means of microcosm experiments. Finally, in chapter 5 we discuss the significance of these results as a first step in our aim to understand the effects of turbulence on plankton in natural systems.

References

- Agrawal, Y.C., Terray, E.A., Donelan, M.A., Hwang, P.A., Williams III, A.J., Drennan, W.M., Kahma, K.K. and S.A. Kitaigorodski. 1992. Enhanced dissipation of kinetic energy beneath surface waves. *Nature*. **359**: 219-220.
- Alcaraz, M., Marrasé, C., Peters, F., Arin, L. and A. Malits. 2002. Effects of turbulence conditions on the balance between production and respiration in marine planktonic communities. *Mar. ecol., Prog. ser.* **242**: 63-71.
- Alcaraz, M., Saiz, E., Marrasé C. and Vaqué D. 1988. Effects of turbulence on the development of phytoplankton biomass and copepod populations in marine microcosms. *Mar. ecol., Prog. ser.* **49**: 117-125.
- Ambühl, H. 1960. Die Bedeutung der Strömung als ökologischer Faktor. *Schweiz. Z. Hydrol.* **21**: 133-264.
- Arin, L., Marrasé, C., Maar, M., Peters, F., Sala, M.M. and M. Alcaraz. 2002. Combined effects of nutrients and small-scale turbulence in a microcosm experiment. I. Dynamics and size distribution of osmotrophic plankton. *Aquat. microb. ecol.* **29**: 51-61.
- Azam, F., Fenchel, T., Field, J.G., Gray, J.S., Meyer-Reil L.A. and F. Thingstad. 1983. The Ecological Role of Water-Column Microbes in the Sea. *Mar. ecol., Prog. ser.* **10**: 257-263.
- Banavar, J.R., Damuth, J., Maritan, A. and A. Rinaldo. 2002. Supply-demand balance and metabolic scaling. *Proc. Natl Acad. Sci. USA.* **99**: 10506-10509.
- Berdalet, E. 1992. Effects of turbulence on the marine dinoflagellate *Gymnodinium nelsonii*. *J. phycol.* **28**: 267-272.
- Berdalet, E. and M. Estrada. 1993. Effects of turbulence on several dinoflagellate species, 737-740. In Smayda, T.J. and Y. Shimizu [eds.], *Toxic phytoplankton blooms in the sea*. Elsevier Science Publishers B.V.
- Berdalet, E. and M. Estrada. 2005. Effects of small-scale turbulence on the physiological functioning of marine microalgae, 459-500. In Subba Rao, D.V. [ed.], *Algal cultures, analogues of blooms and applications*. Science Publishers, Enfield (NH), USA.
- Berman, T. and B. Shteinman. 1998. Phytoplankton development and turbulent mixing in Lake Kinneret (1992-1996). *J. plankton res.* **20**: 709-726.
- Bratbak, G. and T.F. Thingstad. 1985. Phytoplankton-bacteria interactions - An apparent paradox - Analysis of a model system with both competition and commensalism. *Mar. ecol., Prog. ser.* **25**: 30.

- Chisholm, S.W. 2000. Oceanography - Stirring times in the Southern Ocean. *Nature*. **407**: 685-687.
- Cloern, J.E. 1987. Turbidity as a control on phytoplankton biomass and productivity in estuaries. *Cont. shelf res.* **7**: 1367-1381.
- Cloern, J.E. 2001. Our evolving conceptual model of the coastal eutrophication problem. *Mar. ecol., Prog. ser.* **210**: 223-253.
- Colomer, J., Peters, F. and C. Marrasé. 2005. Experimental analysis of coagulation of particles under low-shear flow. *Water res. (Oxf.)*. **39**: 2994-3000.
- Cotner, J.B. 2000. Intense winter heterotrophic production stimulated by benthic resuspension. *Limnol. Oceanogr.* **45**: 1672-1676.
- Cózar, A. and F. Echevarría. 2005. Size structure of the planktonic community in microcosms with different levels of turbulence. *Sci. mar.* **69**: 187-197.
- Csanady, G. 1989. Energy Dissipation and Upwelling in a Western Boundary Current. *J. phys. oceanogr.* **19**: 462-473.
- D'Asaro E.A. and G.T. Dairiki. 1997. Turbulence intensity measurements in a wind-driven mixed layer. *J. phys. oceanogr.* **27**: 2009-2022.
- Dade, W.B. 1993. Near bed turbulence and hydrodynamic control of diffusional mass-transfer at the sea-floor. *Limnol. Oceanogr.* **38**: 52-69.
- Donaghay, P.L. and E. Klos. 1985. Physical, chemical and biological responses to simulated wind and tidal mixing in experimental marine ecosystems. *Mar. ecol., Prog. ser.* **26**: 45.
- Denman, K.L. and T. Platt. 1976. Variance spectrum of phytoplankton in a turbulent ocean. *J. mar. res.* **34**: 601.
- Denman, K.L. and A.E. Gargett. 1983. Time and space scales of vertical mixing and advection of phytoplankton in the upper ocean. *Limnol. Oceanogr.* **28**: 801-815.
- Dewey, R.K. and J. Moum. 1990. Enhancement of fronts by vertical mixing. *J. geophys. res.* **95**: 9433-9445.
- Duarte, C.M., Agustí, S. and N.S.R. Agawin. 2000. Response of a Mediterranean phytoplankton community to increased nutrient inputs: a mesocosm experiment. *Mar. ecol., Prog. ser.* **195**: 61-70.
- Eppley, R.W., Koeller, P. and G.T. Wallace Jr. 1978. Stirring influences the phytoplankton species composition within enclosed columns of coastal sea water. *J. exp. mar. biol. ecol.* **32**: 219-239.
- Estrada, M., Alcaraz, M. and C. Marrasé. 1987. Effects of turbulence on the composition of phytoplankton assemblages in marine microcosms. *Mar. ecol., Prog. ser.* **38**: 267-281.
- Estrada, M., Marrasé, C. and M. Alcaraz. 1988. Phytoplankton response to intermittent stirring and nutrient addition in marine microcosms. *Mar. ecol., Prog. ser.* **48**: 225-234.
- Estrada, M. and Berdalet E. 1997. Phytoplankton in a turbulent world. *Sci. mar.* **61**: 125-140.
- Estrada, M. and E. Berdalet. 1998. Effects of turbulence on phytoplankton, 601-618. In Anderson, D. M., Cembella, A. D. and G. M. Hallegraeff [eds.], *Physiological ecology of harmful algal blooms*. Springer-Verlag Berlin Heidelberg.
- Field, C.B., Behrenfeld, M.J., Randerson, J.T. and P. Falkowski. 1998. Primary production of the biosphere: Integrating terrestrial and oceanic components. *Science*. **281**: 237-240.
- Franks, P.J.S. 2001. Phytoplankton blooms in a fluctuating environment: the roles of plankton response time scales and grazing. *J. plankton res.* **23**: 1441.
- Franks, P.J.S. 2005. Plankton patchiness, turbulent transport and spatial spectra. *Mar. ecol., Prog. ser.* **294**: 301-305.
- Gargett, A.E. 1989. Ocean turbulence. *Annu. rev. fluid mech.* **21**: 419-451.
- Gargett, A. and P. Donaghay. 2003. Turbulence mixing and biophysical interactions. In: Regional Cabled Observatory Network (of Networks), Report of the Cabled Regional Observatory Workshop (http://www.geo-prose.com/cabled_wksp/pdfs/reconn_rpt.3.2.04.pdf, downloaded 27/07/05).
- Garstecki, T. and H. Arndt. 2000. Seasonal abundances and community structure of benthic rhizopods in shallow lagoons of the southern Baltic Sea. *Eur. j. protistol.* **36**: 103-115.
- Gemmrich, J.R. and D.M. Farmer. 1999. Near-surface turbulence and thermal structure in a wind-driven sea. *J. phys. oceanogr.* **29**: 480-499.
- Gemmrich, J.R. and D.M. Farmer. 2004. Near-surface turbulence in the presence of breaking waves. *J. phys. oceanogr.* **34**: 1067-1086.
- Ghosal, S., Rogers, M. and A. Wray. 2000. The turbulent life of phytoplankton. Center for Turbulence Research, Proceedings of the Summer Program 2000. 31-45.
- Gibson, C.H. and W.H. Thomas. 1995. Effects of turbulence intermittency on growth inhibition of a red

- tide dinoflagellate, *Gonyaulax polyedra* Stein. *J. geophys. res.* **100**: 24841-24846.
- Grémare, A., Amoroux, J.M., Cauwet, G., Charles, F., Courties, C., De Bovée, F., Dinet, A., Devenon, J.L., DeMadron, X.D., Ferre, B., Fraunie, P., Joux, F., Lantoine, F., Lebaron, P., Naudin, J.J., Palanques, A., Pujon-Pay, M. and L. Zudaire. 2003. The effects of a strong winter storm on physical and biological variables at a shelf site in the Mediterranean. *Oceanol. acta.* **26**: 407-419.
- Haurly, L.R., Yamazaki, H. and E.C. Itsweire. 1990. Effects of turbulent shear flow on zooplankton distribution. *Deep-sea res.* **37**: 447-461.
- Haurly, L.R., Yamazaki, H. and C.L. Fey. 1992. Simultaneous measurements of small-scale physical dynamics and zooplankton distributions. *J. plankton res.* **14**: 513-530.
- Hopfinger, E. and J. Toly. 1976. Spatially decaying turbulence and its relation to mixing across density interfaces. *J. fluid mech.* **78**: 175-188.
- Howarth, R.W., Butler, T., Lunde, K., Swaney, D. and C.H. Chu. 1993. Turbulence and planktonic nitrogen fixation: a mesocosm experiment. *Limnol. Oceanogr.* **38**: 1696-1711.
- Huisman, J., Arrayás, M., Ebert, U. and B. Sommeijer. 2002. How do sinking phytoplankton species manage to persist? *Am. nat.* **159**: 245-254.
- Huisman, J., vanOostveen, P. and F.J. Weissing. 1999. Critical depth and critical turbulence: Two different mechanisms for the development of phytoplankton blooms. *Limnol. Oceanogr.* **44**: 1781-1787.
- Hutchinson, G.E. 1961. The Paradox of the Plankton. *Am. nat.* **95**: 137-145.
- IPCC. 2007. Climate change 2007: The physical science basis. Summary for policymakers. <http://www.ipcc.ch/SPM2feb07.pdf>.
- Jackson, G. 1990. A model of the formation of marine algal flocs by physical coagulation processes. *Deep-sea res.* **37**: 1197-1211.
- Jiménez, J. 1997. Oceanic turbulence at millimeter scales. In: C. Marrasé, E. Saiz and J.M. Redondo [eds.], *Lectures on Plankton and Turbulence*, *Sci. Mar.* **61** (suppl. 1): 47-56.
- Jou, D. 1997. Intermittent turbulence: A short introduction. In: C. Marrasé, E. Saiz and J.M. Redondo [eds.], *Lectures on Plankton and Turbulence*, *Sci. Mar.* **61** (suppl. 1): 205-228.; 57-62.
- Juhl, A.R., Velazquez, V. and M.I. Latz. 2000. Effect of growth conditions on flow-induced inhibition of population growth of a red-tide dinoflagellate. *Limnol. Oceanogr.* **45**: 905-915.
- Juhl, A.R., Trainer, V.L. and M.I. Latz. 2001. Effect of fluid shear and irradiance on population growth and cellular toxin content of the dinoflagellate *Alexandrium fundyense*. *Limnol. Oceanogr.* **46**: 764.
- Juhl, A., Latz, M.I. 2002. Mechanisms of fluid shear-induced inhibition of population growth in a red-tide dinoflagellate. *J. phycol.* **38**: 683-694.
- Jumars, P.A., Deming, J.W., Hill, P.S., Karp-Boss, L., Yager, P.L. and W.B. Dade. 1993. Physical constraints on marine osmotrophy in an optimal foraging context. *Mar. Microb. Food Webs.* **7**: 121-159.
- Kolmogorov, A.N. 1941. The local structure of turbulence in incompressible viscous fluid for very large Reynolds' numbers. *Dokl. Akad. Nauk. SSSR.* **30**: 301-305. (Reprinted in *Proc. Roy. Soc. Lond. A.* 434: 9-13, 1991.)
- Karp-Boss, L., Boss, E. and P.A. Jumars. 1996. Nutrient fluxes to planktonic osmotrophs in the presence of fluid motion. *Oceanography and marine Biology: An Annual review.* **34**: 71-107.
- Karp-Boss, L., Boss, E. and P.A. Jumars. 2000. Motion of dinoflagellates in a simple shear flow. *Limnol. Oceanogr.* **45**: 1594-1602.
- Kemp, W.M. and W.J. Mitsch. 1979. Turbulence and phytoplankton diversity: A general model of the "paradox of plankton". *Ecol. model.* **7**: 201-222.
- Kitaigorodskii, S.A., Donelan M.A, Lumley J.L. and Terray E.A. 1983. Wave turbulence interactions in the upper ocean. 2. Statistical characteristics of wave and turbulent components of the random velocity-field in the marine surface-layer. *J. phys. oceanogr.* **13**: 1988-1999.
- Kjørboe, T. 1997. Small-scale turbulence, marine snow formation, and planktivorous feeding. In: C. Marrasé, E. Saiz and J.M. Redondo [eds.], *Lectures on Plankton and Turbulence*, *Sci. Mar.* **61** (suppl. 1): 141-158.
- Kjørboe, T. 1993. Turbulence, phytoplankton cell size, and the structure of pelagic food webs. *Adv. Mar. Biol.* **29**: 1-72.
- Legendre L. and J. Le Fèvre. 1995. Microbial food webs and the export of biogenic carbon in oceans. *Aquat. microb. ecol.* **9**: 69-77.
- Litchman, E. 1998. Population and community responses of phytoplankton to fluctuating light. *Oecologia.* **117**: 257.

- Litchman, E. 2000. Growth rates of phytoplankton under fluctuating light. *Freshw. biol.* **44**: 235.
- Maar, M., Arín, L., Simó, R., Sala, M.M., Peters, F. and C. Marrasé. 2002. Combined effects of nutrients and small-scale turbulence in a microcosm experiment. II. Dynamics of organic matter and phosphorus. *Aquat. microb. ecol.* **29**: 63-72.
- MacKenzie, B.R. and W.C. Leggett. 1993. Wind-based models for estimating the dissipation rates of turbulent energy in aquatic environments: empirical comparisons. *Mar. ecol., Prog. ser.* **94**: 207-216.
- MacKenzie, B.R. and T. Kiørboe. 1995. Encounter rates and swimming behaviour of pause-travel and cruise larval fish predators in calm and turbulent laboratory environments. *Limnol. Oceanogr.* **40**: 1278-1289.
- Malits, A., Peters, F., Bayer-Giraldi, M., Marrasé, C., Zoppini, A., Guadayol, Ò. and M. Alcaraz. 2004. Effects of Small-Scale Turbulence on Bacteria: A Matter of Size. *Microb. Ecol.* **48**: 287-299.
- Mann, K.H. and J.R.N. Lazier. 1996. Dynamics of marine ecosystems. Biological-physical interactions in the oceans. 2nd ed. Blackwell Publishing.
- Margalef, R. 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanol. acta.* **1**: 493-509.
- Margalef, R., M. Estrada and D. Blasco. 1979. Functional morphology of organisms involved in red tides, as adapted to decaying turbulence, 89-94. In Taylor, D.L. and H.H. Selinger [eds.], *Toxic dinoflagellate blooms*. Elsevier/North Holland.
- Margalef, R. 1991. Teoría de los sistemas ecológicos. ed. Publicacions Universitat de Barcelona.
- Marrasé, C., J.H. Costello, T. Granata and J.R. Strickler. 1990. Grazing in a turbulent environment: Energy dissipation, encounter rates, and efficacy of feeding currents in *Centropages hamatus*. *Proc. Natl. Acad. Sci. USA.* **87**: 1653-1657.
- McWilliams, J.C. and Sullivan, P.P., Moeng, C. 1997. Langmuir turbulence in the ocean. *J. fluid mech.* **334**: 1-30.
- Moeseneder, M.M. and G.J. Herndl. 1995. Influence of turbulence on bacterial production in the sea. *Limnol. Oceanogr.* **40**: 1466-1473.
- Mountain, D.G. and M.H. Taylor. 1996. Fluorescence structure in the region of the tidal mixing front on the southern flank of Georges Bank. *Deep-sea res., Part 2, Top. stud. oceanogr.* **43**: 1831-1853.
- NRC, Committee on Understanding Oil Spill Dispersants: Efficacy and Effects. 2005. Oil Spill Dispersants: Efficacy and Effects. <http://www.nap.edu/books/030909562X/html/>.
- Oakey, N.S. 1985. Statistics of mixing parameters in the upper layer ocean during JASIN Phase 2. *J. phys. oceanogr.* **15**: 1662-1675.
- Oakey, N.S. and J. Elliott. 1982. Dissipation within the surface mixed layer. *J. phys. oceanogr.* **12**: 171-185.
- Osborn, T.R. 1974. Vertical profiling of velocity microstructure. *J. phys. oceanogr.* **4**: 109-115.
- Oviatt, C.A. 1981. Effects of different mixing schedules on phytoplankton, zooplankton and nutrients in marine microcosms. *Mar. ecol., Prog. ser.* **4**: 67.
- Oviatt, C.A., Hunt, C.D., Vargo, G.A. and K.W. Kopchynski. 1981. Simulation of a storm event in marine microcosms. *J. mar. res.* **39**: 626.
- Peters, F. and T. Gross. 1994. Increased grazing rates of microplankton in response to small-scale turbulence. *Mar. ecol., Prog. ser.* **115**: 299-307.
- Peters, F. and J.M. Redondo. 1997. Turbulence generation and measurement: Application to studies on plankton. In: C. Marrasé, E. Saiz and J.M. Redondo [eds.], *Lectures on Plankton and Turbulence, Sci. Mar.* **61** (suppl. 1): 205-228.
- Peters, F., Marrasé, C., Gasol, J.M., Sala, M.M. and L. Arin. 1998. Effects of turbulence on bacterial growth mediated through food web interactions. *Mar. ecol., Prog. ser.* **172**: 293-303.
- Peters, F. and C. Marrasé. 2000. Effects of turbulence on plankton: an overview of experimental evidence and some theoretical considerations. *Mar. ecol., Prog. ser.* **205**: 291-306.
- Peters, F., Marrasé, C., Havskum, H., Rassoulzadegan, F., Dolan, J., Alcaraz, M. and J.M. Gasol. 2002. Turbulence and the microbial food web: effects on bacterial losses to predation and on community structure. *J. plankton res.* **24**: 321-331.
- Petersen, J.E., Sanford, L.P. and W.M. Kemp. 1998. Coastal plankton responses to turbulent mixing in experimental ecosystems. *Mar. ecol., Prog. ser.* **171**: 23-41.
- Platt, T. 1972. Local phytoplankton abundance and turbulence. *Deep-sea res. oceanogr. abstr.* **19**: 183-187.
- Pollinger, U. and E. Zemel. 1981. In situ and experimental evidence of the influence of turbulence on cell division processes of *Peridinium cinctum* forma *westii* (Lemm.) Lefèvre. *Br. Phycol. J.* **16**: 281-287.

- Pomeroy, L.R. 1974. The Ocean's Food Web, A Changing Paradigm. *BioScience*. **24**: 499-504.
- Powell, T. M. and A. Okubo. 1994. Turbulence, diffusion and patchiness in the sea. *Philos. trans. R. Soc. Lond., B Biol. sci.* **343**: 11-18.
- Redfield, A.C. 1934. On the proportions of organic derivatives in sea water and their relation to the composition of plankton, 170-192. In *James Johnstone Memorial Volume*.
- Redfield, A.C., Ketchum, B.H. and F.A. Richards. 1963. The influence of organisms on the composition of sea-water, 26-77. In Hill, M.N. [ed.], *The Sea*. Wiley, NY.
- Reynolds, C.S., Wiseman, S.W., Godfrey, B.M. and C. Butterwick. 1983. Some effects of artificial mixing on the dynamics of phytoplankton populations in large limnetic enclosures. *J. plankton res.* **5**: 203-234.
- Richardson, T.L. and G.A. Jackson. 2007. Small Phytoplankton and Carbon Export from the Surface Ocean. *Science*. **315**: 838-840.
- Rivkin, R.B. and L. Legendre. 2001. Biogenic carbon cycling in the upper ocean: Effects of microbial respiration. *Science*. **291**: 2398-2400.
- Ross, O.N. 2006. Particles in motion: How turbulence affects plankton sedimentation from an oceanic mixed layer. *Geophys. res. lett.* **33**: L10609.
- Rothschild, B.J. and T.R. Osborn. 1988. Small-scale turbulence and plankton contact rates. *J. plankton res.* **10**: 465-474.
- Ruiz, J. 1996. The role of turbulence in the sedimentation loss of pelagic aggregates from the mixed layer. *J. mar. res.* **54**: 385-406.
- Ruiz, J., Garcia, C.M. and J. Rodríguez. 1996. Sedimentation loss of phytoplankton cells from the mixed layer: effects of turbulence levels. *J. plankton res.* **18**: 1727-1734.
- Ruiz, J., Macías, D. and F. Peters. 2004. Turbulence increases the average settling velocity of phytoplankton cells. *Proc. Natl. Acad. Sci. USA*. **101**: 17720-17724.
- Saiz, E. and M. Alcaraz. 1992. Enhanced excretion rates induced by small-scale turbulence in *Acartia* (Copepoda: Calanoida). *J. plankton res.* **14**: 681-689.
- Saiz, E., Alcaraz, M. and G.A. Paffenhofer. 1992. Effects of small-scale turbulence on feeding rate and gross-growth efficiency of three *Acartia* species (Copepoda: Calanoida). *J. plankton res.* **14**: 1085-1097.
- Saiz, E. and T. Kiørboe. 1995. Predatory and suspension feeding of the copepod *Acartia tonsa* in turbulent environments. *Mar. ecol., Prog. ser.* **122**: 147-158.
- Samuelsson, K., Berglund, J., Haecky, P. and A. Andersson. 2002. Structural changes in an aquatic microbial food web caused by inorganic nutrient addition. *Aquat. microb. ecol.* **29**: 29-38.
- Sanford, L.P. 1997. Turbulent mixing in experimental ecosystem studies. *Mar. ecol., Prog. ser.* **161**: 265-293.
- Shimeta, J., Jumars, P.A. and E.J. Lessard. 1995. Influences of turbulence on suspension feeding by planktonic protozoa; experiments in laminar shear fields. *Limnol. Oceanogr.* **40**: 845-859.
- Smayda, T. 2002. Turbulence, watermass stratification and harmful algal blooms: an alternative view and frontal zones as "pelagic seed banks". *Harmful Algae*. **1**: 95-112.
- Smetacek, V.S. 1985. Role of sinking in diatom life-history cycles - ecological, evolutionary and geological significance. *Mar. biol.* **84**: 251.
- StLaurent, L. C., Simmons, H.L. and S.R. Jayne. 2002. Estimating tidally driven mixing in the deep ocean. *Geophys. res. lett.* **29**: 21-20.
- Stips, A., Burchard, H., Bolding, K., Prandke, H., Simon A. and A. Wüest. 2005. Measurement and simulation of viscous dissipation in the wave affected surface layer *Deep-sea res., Part 2, Top. stud. oceanogr.* **52**: 1133-1155.
- Sullivan, J.M. and E. Swift. 2003. Effects of small-scale turbulence on net growth rate and size of ten species of marine dinoflagellates. *J. phycol.* **39**: 83-94.
- Sun, H.L. and E. Kunze. 1999. Internal wave-wave interactions. Part II: Spectral energy transfer and turbulence production. *J. phys. oceanogr.* **29**: 2905-2919.
- Sundby, S. and P. Fossum. 1990. Feeding conditions of Arcto-norwegian cod larvae compared with the Rothschild-Osborn theory on small-scale turbulence and plankton contact rates. *J. plankton res.* **12**: 1153-1162.
- Svensen, C., Egge, J.K. and J.E. Stiansen. 2001. Can silicate and turbulence regulate the vertical flux of biogenic matter? A mesocosm study. *Mar. ecol., Prog. ser.* **217**: 67-80.
- Sverdrup, H.U. 1953. On the conditions for the vernal blooming of phytoplankton. *J. Cons. Perm. Int. Exp. Mer.* **18**: 287-295.
- Taylor, G. 1935. Statistical theory of turbulence. *Proc. - Royal Soc., Math. phys. eng. sci.* **151**: 421-444.

- Tennekes, H. and J.L. Lumley. 1972. A first course in turbulence. MIT Press, Cambridge, MA.
- Terray, E.A., Donelan, M.A., Agrawal, Y.C., Drennan, W.M., Kahma, K.K., Williams, A.J.I., Hwang, P.A. and S.A. Kitaigorodskii. 1996. Estimates of kinetic energy dissipation under breaking waves. *J. phys. oceanogr.* **26**: 792-807.
- Thingstad, T.F., Skjoldal, E.F. and R.A. Bohne. 1993. Phosphorus cycling and algal-bacterial competition in Sandsfjord, Western Norway. *Mar. ecol., Prog. ser.* **99**: 259.
- Thingstad, T.F. and F. Rassoulzadegan. 1995. Nutrient limitations, microbial food webs, and 'biological C-pumps': suggested interactions in a P-limited Mediterranean. *Mar. ecol., Prog. ser.* **117**: 299-306.
- Thomas, W.H. and C.H. Gibson. 1990. Quantified small-scale turbulence inhibits a red tide dinoflagellate, *Gonyaulax polyedra* Stein. *Deep-sea res.* **37**: 1583-1593.
- Thomas, W.H. and C.H. Gibson. 1992. Effects of quantified small-scale turbulence on the dinoflagellate *Gymnodinium sanguineum* (*splendens*): contrasts with *Gonyaulax* (*Lyngulodinium*) *polyedra*, and the fishery implication. *Deep-sea res.* **39**: 1429-1437.
- Thomas, E.H., Vernet, M. and C.H. Gibson. 1995. Effects of small-scale turbulence on photosynthesis, pigmentation, cell division, and cell size in the marine dinoflagellate *Gonyaulax polyedra* (Dinophyceae). *J. phycol.* **31**: 50-59.
- Thomas, W.H., Tynan, C.T. and C. Gibson. 1997. Turbulence-phytoplankton interrelationships, 283-324. In Round, F.E. and D.J. Chapman [eds.], *Progress in phycological research*. Biopress Ltd.
- Thorpe, S.A. 2004. Recent developments in the study of ocean turbulence. *Annu. rev. earth planet. sci.* **32**: 91-109.
- Turner, J.S. 1973. Buoyancy effects in fluids. Cambridge University Press, London.
- Wyatt, T. and J. Horwood. 1973. Model which generates red tides. *Nature.* **244**: 240.
- Yamazaki, H., Mitchell, J.G., Seuront, L., Wolk, F. and H. Li. 2006. Phytoplankton microstructure in fully developed oceanic turbulence. *Geophys. res. lett.* **33**: L01603.
- Zirbel, M.J., Veron, F. and M.I. Latz. 2000. The reversible effect of flow on the morphology of *Ceratocorys horrida* (Peridinales, *Dinophyta*). *J. phycol.* **36**: 46-58.