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4.6. Turbulence and plankton dynamics in a warmer ocean

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Differences in the temperature and salt content of the water, which determine its density, wind energy and the rotation of the earth drive a complex and variable ocean circulation system. The mechanical energy thus generated, essential for maintaining the dynamics of marine ecosystems, generates turbulent eddies that divide into smaller eddies, and so on until they reach a size (the Kolmogorov scale) at which viscosity overcomes inertia.

Turbulence: characteristics and effects on plankton

The role of turbulent movements at the largest scales (the meso- and macroscale, from metres to hundreds of kilometres) is mainly one of transport. At the smallest scales, of the order of millimetres (small scale and microscale turbulence), the velocity gradients generated by turbulence directly affect particles in the size range of plankton organisms, a community suspended in the water column that includes practically all biological groups, from viruses and bacteria to fish larvae.

The organic matter that fuels the marine food webs is produced by phytoplankton or "plant plankton", which includes unicellular algae of very diverse characteristics (Figure 1). Factors ranging from fisheries production to CO_2 capture by the marine ecosystem are largely dependent on the phytoplankton groups that dominate in the community. The seasonal changes of phytoplankton throughout the annual cycle were explained by Ramón Margalef through a conceptual model. In the graphical representation of the model, known internationally as the *Margalef Mandala*, the different biological forms of phytoplankton (groups that share certain functional characteristics) are located in a plane in which the coordinate axes are the intensity of the turbulence and the concentration of nutrients.

Questions arising from Margalef's Mandala have given birth to a fruitful line of work of the Institut de Ciències del Mar (ICM) on the effects of small-scale turbulence on marine plankton as a whole, and led to the holding of the first international course on the theme: *Lectures on Plankton and Turbulence*, funded by the EU and coordinated by scientists from the ICM, the University of Barcelona and other scientific organizations (Marrasé *et al.* 1997).

As the effects of turbulence cannot be isolated from those caused by other factors in the natural environment, laboratory experimentation is necessary. Tanks or aquariums that contain amounts ranging from litres (microcosms) to cubic metres (mesocosms) of seawater are used to control the intensity of turbulence and the conditions of temperature, nutrients and light, as well as the species or communities of plankton to be studied (Estrada *et al.* 1988).

Turbulence is important for the selection of biological forms of phytoplankton because it increases the absorption of nutrients by cells or keeps them in suspension in the water column. Turbulence also affects the migratory strategy of dinoflagellates and can have a negative effect when it is very high (Berdalet *et al.* 2007). Changes in its intensity also interact with the motility, shape and size of cells and cell colonies and help to maintain a high specific diversity (Figure 1)

For zooplankton, provided with chemical and movement microsensors, turbulence can

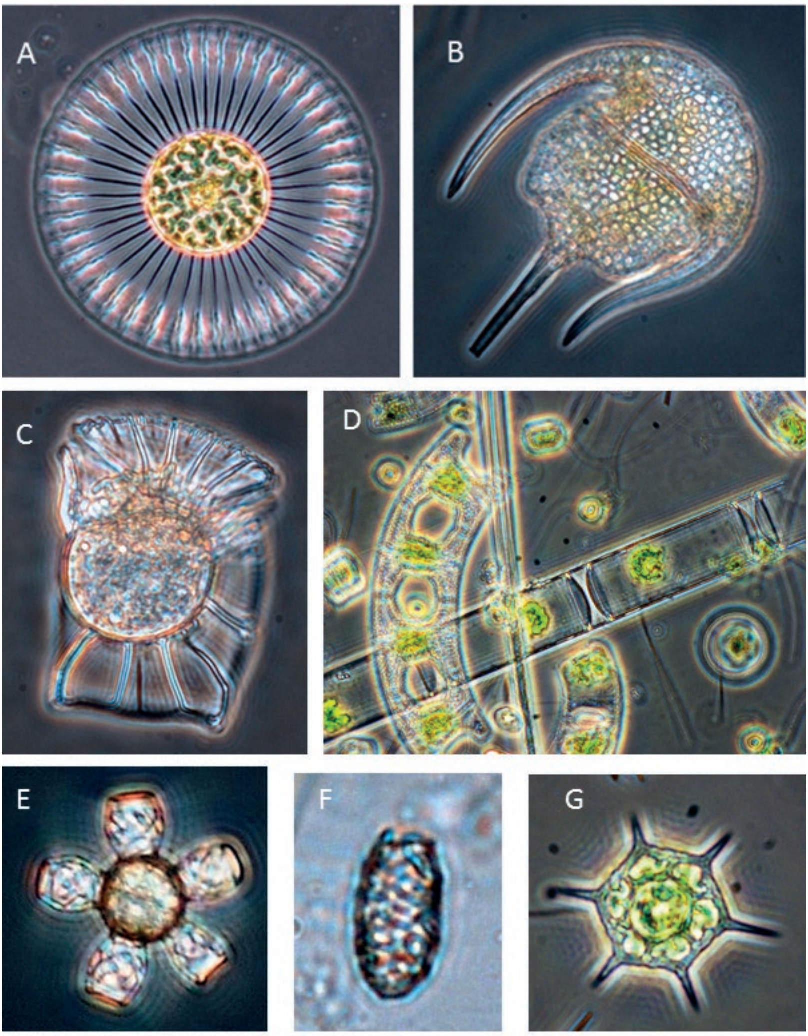

Figure 1. Diversity of forms in phytoplankton (light microscope photographs). A, D, diatoms; B, C, dinoflagellates; E, F, coccolithophores; G, silicoflagellates. The diameter of the cells ranges from little more than about 10 microns in E and F to more than 100 microns in B and C (Photo: M. Estrada).

produce an increase in food intake (greater frequency of contact with food particles), and affect the location of a possible mate by erasing the pheromone track delivered by females as a signal. Water turbulence can also be mistaken with distortions in the water motion generated by prey or predators, inducing attacks or an increase in escape reactions, which have a high metabolic consumption (Figure 2). Other effects of turbulence are changes in the sexual proportion, inducing a greater abundance of males, and the reduction of the average individual size (Saiz 1991).

Turbulence and plankton in a warmer ocean

The climate change that is already underway points to a future ocean that is not only warmer but also exposed to a higher occurrence of turbulence-generating, highly energetic atmospheric events. Temperature and turbulence present analogies (temperature, molecular disorder; turbulence, hydrodynamic disorder), and both trigger very similar responses in some basic properties and activities of organisms.

Both turbulence and temperature increases induce a higher metabolic activity, an intensification of ingestion rates and a reduction in the average individual size. The latter effect has cumulative consequences on metabolism, since biomass-specific metabolic rates are inversely proportional to size.

While it is known that the vital functions are only possible between a certain range of temperatures that is inversely proportional to the complexity of the organism or function, and that the response of the activity is bell-shaped (it increases with temperature until an optimal value and then decreases), the dynamics of the processes in the case of turbulence is unknown.

Then again, laboratory experiments show that turbulence increases the quotient between the carbon produced by phytoplankton and that breathed by the whole plankton community (Alcaraz *et al.* 2002). Therefore, although part of the consequences of the increase in temperature may be amplified by the similar effects arising from turbulence, the role of the latter in the production/respiration balance introduces a new question. Whatever the case may be, it is clear that turbulence must be taken into account in predictive models of a warmer future ocean.

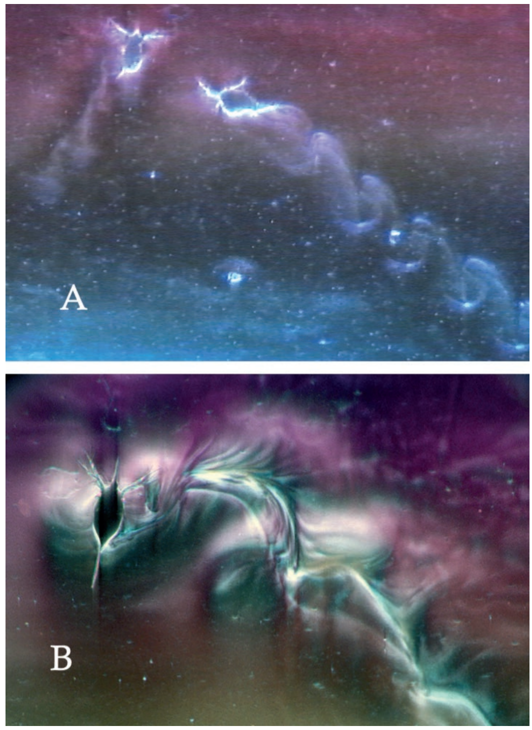

Figure 2. Hydrodynamic tracks created by zooplankton swimming. A, from a carnivorous copepod chasing a prey, by its prey before perceiving the predator's signal and escaping. B, escape reaction of the prey, a freshwater cladoceran (Schlieren optics, Photo: J.R. Strickler).

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